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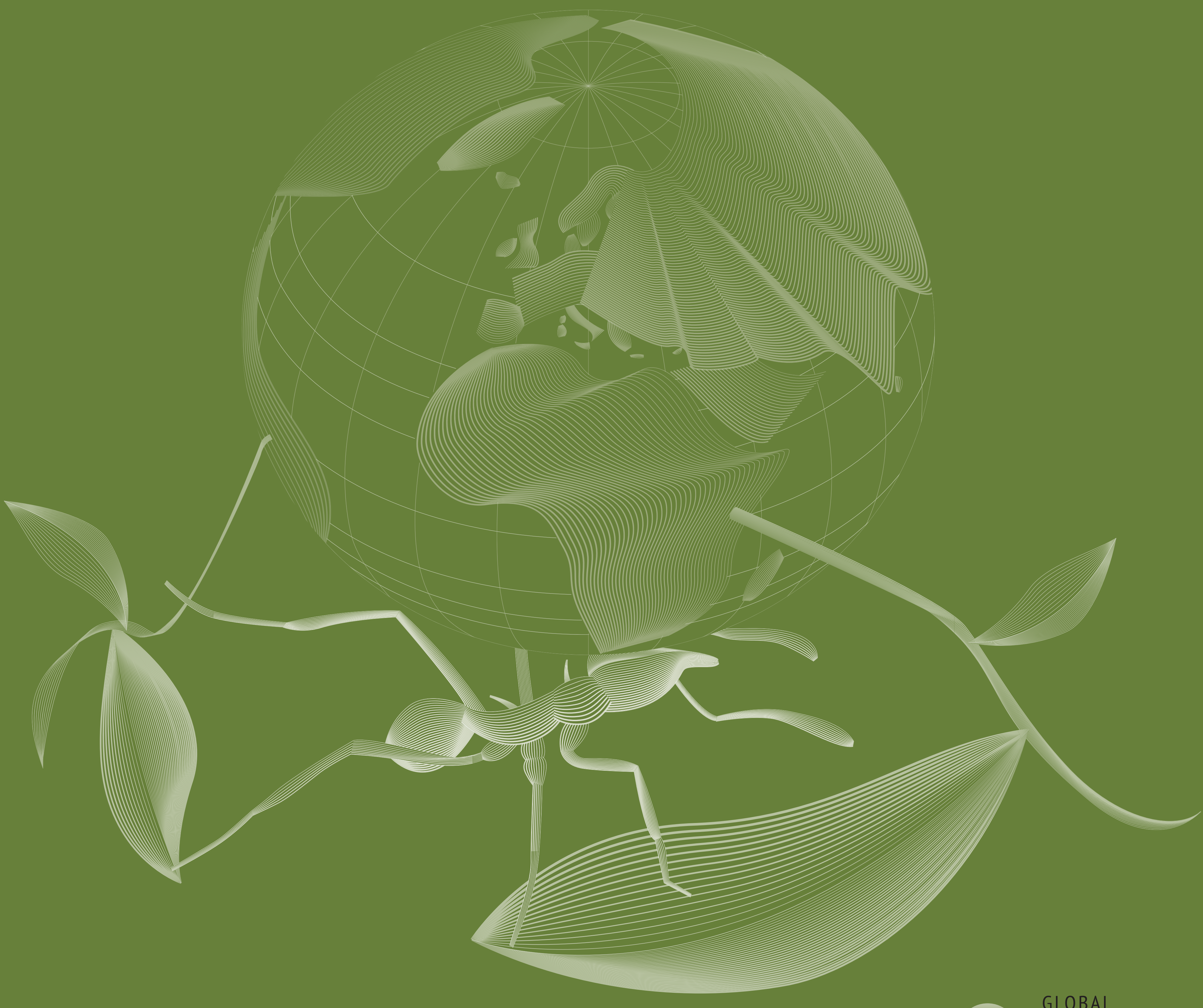
GLOBAL SOIL BIODIVERSITY ATLAS



GLOBAL SOIL BIODIVERSITY INITIATIVE

Joint Research Centre

European Commission

GLOBAL SOIL BIODIVERSITY ATLAS

Supporting the EU Biodiversity Strategy and the Global Soil Biodiversity Initiative: preserving soil organisms through sustainable land management practices and environmental policies for the protection and enhancement of ecosystem services

GLOBAL SOIL BIODIVERSITY INITIATIVE

2015 International Year of Soils

Joint Research Centre

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Hallett; (SI) Stu's Images; (SJ) S. James; (SJA) S. Jarvis; (SJE) S. Jeffery; (SJF) S.J. Fonte; (SJR) S. Jurvetson; (SJS) S. Justis; (SK) S. Kaynas; (SL) S. Lough; (SLA) slappytheseal; (SLS) S.L. Stürmer; (SM) S. McCann; (SMA) S. Marotta; (SME) S. Means; (SMI) S. Miller; (SMM) S.M. Emery; (SMNG) Senckenberg Museum fuer Naturkunde Görlitz; (SMO) S. Mojumder; (SNA) snapp3r; (SNZ) Smithsonian's National Zoo; (SO) S. O'Neill; (SOA) S. Oats; (SOG) Son of Groucho; (SP) Sponk; (SPO) S. Pérez-Ortega; (SPR) S. Porter; (SPS) Science and Plants for Schools; (SRA) S. Rae; (SR-E) S. Rodríguez Echeverría; (SRN) S. Rankin; (SS) S. Shimano; (SSA) S. Salisbury; (SSC) Soil Science; (SSH) S. Shattuck; (SSN) S. Snapp; (SSSA) Soil Science Society of America; (SSW) S. Swanwick; (ST) S. Texturas; (STH) S. Thurston; (SUS) SuSanA Secretariat; (SZ) S. Zaki; (SZO) S. Zoia; (TAT) Tatters; (TBL) The British Library; (TC) T.H. Cooper; (TD) T. Decaëns; (TE) TinaEnviro; (TEF) T. Efthimiadis; (TEI) T. Eickhorst; (TF) T. Fraser; (TFG) T. Fogg; (TFO) T. Först; (TFTF) Trees For The Future; (TG) T. Gallali; (TGA) T. Galvez; (TGA) T. Gage; (TH) T. Harada; (TI) T. Itoh; (TIW) T. Iwane; (TJB) T.J. Beveridge; (TK) T. Komatsu; (TO) Torpe; (TOR) torbakhopper; (TPF) T.P. Farias; (TR) T. Ryan; (TRA) T. Rajeev; (TS) T. Samoff; (TSC) T. Sheerman-Chase; (TSL) T. Slotta; (TT) T. Tsunoda; (TTJ) T. The Jaguar; (TWA) T. Waters; (UCSFMC) UCSF Medical Center; (UFLA) Federal University of Lavras; (UKGP) ukgardenphotos; (UM) University of Minnesota; (UMLD) University of Miami Libraries Digital; (UMS) University of Michigan; (UNEP) U.N. Environment Programme; (UNIDO) U.N. Industrial Development Organization; (UNN) U.N. Nielsen; (USB) United Soybean Board; (USDA) U.S. Dept. of Agriculture; (USDE) U.S. Dept. of Education; (USFS) U.S. Forest Service; (USFWS) U.S. Fish and Wildlife Service; (USMG) U.S. Mission Geneva; (VF) V. Felde; (VG) V. Gutekunst; (VH) V. Hampl; (VL) V. Lang; (WANP) Western Arctic National Parklands; (WCL) WorldClim; (WCU) W. Cutler; (WDNR) Wisconsin Dept. of Natural Resources; (WIP) Winniepix; (WJ) W. Jaquith; (WPP) W.P. Pfliegler; (WSM) W. Smith; (WTC) W.T. Cassimiro; (WVDP) W. van der Putten; (WVE) W. van Egmond; (WWF) World Wildlife Fund; (YA) Y. Awoki; (YE) Y. Eglit; (YIF) yiftah-s; (YKN) Y. Knies; (YS) Y. Sekiguchi; (YUNGA) Youth and U.N. Global Alliance; (ZL) Z. Lü.

Soil is alive! Soil is home to millions of different organisms: from microorganisms, such as bacteria and fungi, to macrofauna, such as insects and earthworms. Also, several mammals have a strong link to soil. Organisms living in the soil are many, amazing, smart, important and unique. Soil biodiversity is full of incredible stories. The first ever Global Soil Biodiversity Atlas presents you with an exceptional overview of life living in soils. (LD, AM, GF)

Preface

European Commission

2015 was the United Nations International Year of Soils and, for the first time, soils and the life within them were in the spotlight globally. We are pleased therefore, that an international group of experts and scientists from the European Commission's Joint Research Centre (JRC), in close collaboration with colleagues from the Commission's Directorate-General for the Environment and the Global Soil Biodiversity Initiative, have produced the first ever Global Soil Biodiversity Atlas.

Soils are vital for human survival and underpin many sectors of our economy. It is estimated that 99 % of the world's food comes from the terrestrial environment. But soils are also home to over a quarter of global biodiversity. Millions of soil-dwelling organisms promote essential ecosystem services – from plant growth to food production. They support biodiversity, benefit human health, promote the regulation of nutrient cycles that in turn influence climate, and represent an unexplored capital of natural sources.

Our knowledge of soil life is growing continuously, thanks to recent technological advances and awareness of its value. However, it is estimated that only 1 % of soil microorganism species have been identified. Therefore, understanding the highly complex and dynamic life below ground remains one of the most fascinating challenges facing scientists today. A clearer picture of our soils will allow us to better understand environmental and global climate change processes whilst also exploring possible adaptation strategies.

Pressures on soil organisms are well known. An ever increasing global population, and increased demand for food and fibre lead to intensified agriculture, greater use of fertilisers and pesticides as well as monocultures. Unsustainable agricultural practices, climate change, soil erosion and loss of aboveground diversity all negatively affect organisms that live in soil. To develop actions that will preserve soil life, we need to better understand the consequences of the loss of soil biodiversity.

The Global Soil Biodiversity Atlas raises awareness of the role of soil organisms in sustaining life on our planet, and presents the latest research on soil biodiversity. It is also a major contribution to the EU target of halting the loss of biodiversity and ecosystem services in the EU by 2020, and the goals of the 2030 Agenda for Sustainable Development on sustainable food production and fighting land degradation.

This impressive publication marks a crucial step towards a global coordinated effort to assess life below ground, and highlights the need to improve soil conservation and the diversity of life within it.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

The Global Soil Biodiversity Atlas, with its very engaging and pedagogical presentation, provides non-specialists with access to a vast body of knowledge on the richness and excitement of life beneath our feet. It will contribute to raising awareness about the importance of soil biodiversity for the functioning of our ecosystems, our ecosystem services and ultimately human well-being. This atlas will also represent a relevant contribution to the work carried by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

The IPBES was established in 2012 as a mechanism to provide policy relevant knowledge on biodiversity and ecosystem services in response to requests from policy makers. Its membership currently includes 124 governments.

In 2015, the IPBES initiated an assessment of land degradation and restoration in response to requests from governments and other stakeholders, including the United Nations Convention to Combat Desertification (UNCCD). This assessment will be launched in early 2018. It will review the benefits of avoiding degradation; the concepts and perceptions of land degradation and restoration, according to different worldviews; indirect and direct drivers of degradation processes; the nature and extent of land degradation processes, and the resultant loss or decline in biodiversity and ecosystem structure and functioning; and the impact of changes in land degradation and restoration on the delivery of ecosystem services and human well-being. It will also assess the effectiveness of interventions intended to prevent, halt, reduce and mitigate processes of land degradation and to rehabilitate or restore degraded land and a range of development scenarios, including the consideration of different response options and their implications for land degradation regionally and globally. Finally, guidance will be provided to decision makers on how to address land degradation problems and implement restoration strategies at various levels and scales.

The IPBES is currently performing four regional assessments of biodiversity and ecosystem services in Africa, the Americas, Asia Pacific, Europe and Central Asia. Experts involved in these assessments include, of course, specialists of soil biodiversity. If approved by its Plenary in February 2016, the IPBES will begin a global assessment of biodiversity and ecosystem services, almost 15 years after the Millennium Ecosystem Assessment, to be released in 2019. This assessment will form a contribution to the report of the Convention on Biological Diversity on the implementation of the Strategic Plan 2011-2020 and its 20 Aichi Targets.

By contributing to a better understanding and appreciation of soil biodiversity, this atlas will complement nicely the work of the IPBES, and contribute to our common ultimate goal, which is to better value and protect our biodiversity.

Global Soil Biodiversity Initiative

Our age is one of rapid change, incredible discoveries and big science that revolutionise our understanding of how the world around us works. This first global compilation of soil biodiversity focuses on the rapid acceleration of our knowledge and how this dazzling and spectacular world beneath our feet (from bacteria, through fungi, nematodes, mites, ants and earthworms to recognisable animals such as moles, gophers and reptiles) works together, mostly unseen, to provide us with benefits necessary for life. As with other big science initiatives, the newly launched Global Soil Biodiversity Initiative (GSBI) builds on previous successful national and international programmes: the Human Genome Project, The Brain-mapping Project, the Census of Marine Life, the newer Future Earth sustainability research project, and the SCOPE (Scientific Committee on Problems of the Environment) programme of the International Council for Science. These collaborations fostered new thinking, integration of biodiversity and ecosystem science, recognition of ecosystem services, and the importance of the fusion of molecular, species, and ecosystem information to fully encompass biodiversity.

The White Paper produced from the inaugural GSBI meeting in 2012 in London reiterated that 'Earth's soils are living, dynamic interfaces' and that 'Soil organisms are critical for the maintenance of ecosystem services, such as primary productivity, stable soil structure, regulating pathogens and parasites of plants, animals and humans, and ensuring a functioning and productive soil system'. Despite this, soil biodiversity is usually left out of policy decisions, is often overlooked in big evolution and ecology endeavours, and most people are unaware that life as we know it depends on this biodiversity. This reflects our fragmented knowledge of soil biodiversity globally, which is surprising considering its significance. This is not the biodiversity at the bottom of deep ocean trenches, rather it is the very accessible biodiversity in the upper layer of that 'cold, rocky scum of continent carrying tectonic plates' that is humanity's home.

This first ever Global Soil Biodiversity Atlas (GSBA) is the first major product of the Global Soil Biodiversity Initiative and is the result of a partnership with the European Commission's Joint Research Centre (JRC). Modelled on the European Atlas of Soil Biodiversity, it is an exciting collaboration with contributions from experts in soil biology and ecology from all over the world. The GSBA highlights soil as a habitat for an enormous, but largely unknown, diversity of soil-dwelling organisms that keep both the human population and the planet alive. At its most fundamental, it is a series of amazing photos, maps, charts, tables, statistics, and shared information that scientists, educators, policy makers, and non-specialists alike can use as a toolkit for knowing and understanding soil biodiversity globally. Ultimately though, this atlas is a precursor of the GSBI vision – a multi-dimensional data visualisation tool that demonstrates the complexity of soil biodiversity, its link to ecosystem science and its critical role as a future global resource for all of society.

Karmenu Vella
Commissioner for the Environment, Maritime Affairs and Fisheries
European Commission

Tibor Navracsics
Commissioner for Education, Culture, Youth and Sport
European Commission

Anne Larigauderie
Executive Secretary
Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

Diana H. Wall
Scientific Chair
Global Soil Biodiversity Initiative

Key messages

- Soil is an important habitat for thousand millions of organisms.
- Soil biodiversity is extremely diverse in shapes, colours, sizes and functions.
- Soil biodiversity is globally distributed, from deserts to polar regions through grasslands, forests, urban and agricultural areas.
- Soil biodiversity supports many services essential to human beings: plant growth, water and climate regulation, and disease control, among others.
- Soil biodiversity is increasingly under threat due to several pressures acting on soils.
- Interventions to reduce the impact of threats to soil biodiversity are available and should be widely adopted.
- Policies to protect and value soil biodiversity are still at an early stage and need to be further developed.

Contents

Soil is a natural resource comprised of solids (minerals and organic matter), liquids and gases that is found on the land surface, occupies space, and is characterised by one or both of the following: horizons, or layers, that are distinguishable from the initial material as a result of additions, losses, transfers, and transformations of energy and matter and the ability to support rooted plants in a natural environment. (AB, RHR, TS, USDA, WDNR, USDA/NRCSSD)

Scope of the atlas

'Essentially, all life depends upon the soil ... There can be no life without soil and no soil without life; they have evolved together.'

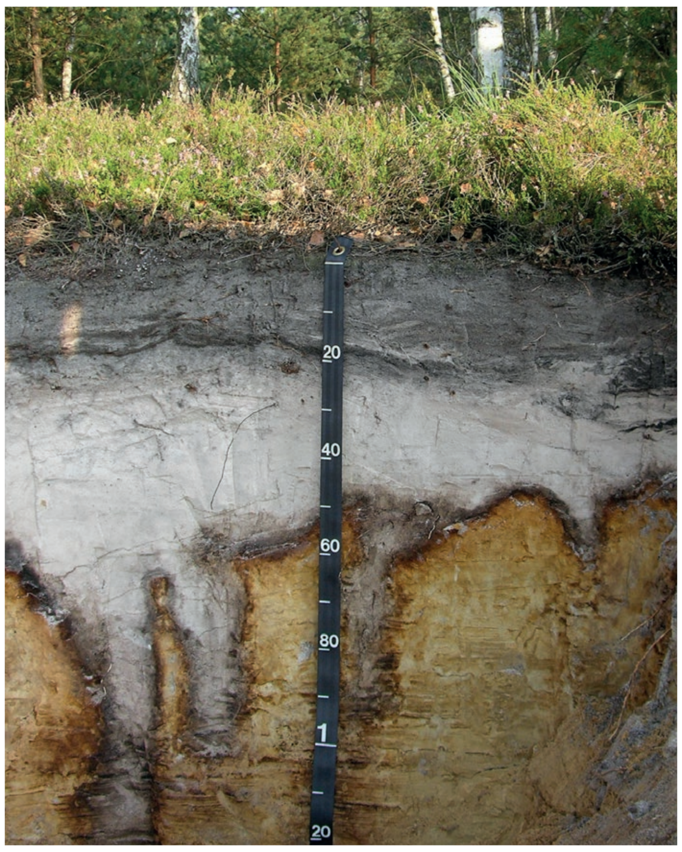
Charles E. Kellogg, USDA Yearbook of Agriculture, 1938.

Soil is composed of living organisms, minerals, organic matter, air and water, and performs a number of key environmental, social and economic services that are vital to life. Supplying water and nutrients to plants, at the same time soil protects water supplies by storing, buffering and transforming pollutants. Soil is an incredible habitat, and it also provides raw materials, preserves our history and reduces the risk of floods. Without soil, the planet as we know it would not function.

However, the importance of soil and the multitude of environmental services that depend on soil properties are not well understood by society at large. Part of the problem is that, with an increasingly urban society, many people have lost contact with the processes that lead to food production. Most people expect to find food on the shelves of supermarkets and have limited or even no appreciation of the roles played by soil. Concepts such as nutrient cycling and organic matter management, that are critical to soil fertility and food production, are a mystery to most of us.

There is very little dialogue between the soil science community and the general public. The majority of soil-related information is geared toward university-level or scientific journals – normally beyond the reach and understanding of the general public. This results in a lack of material to help interested stakeholders appreciate the value of soil and to guide them in preserving this precious resource.

As a consequence, soil tends not to feature in the minds of the public or politicians. However, soil experts are becoming increasingly aware of a greater need to inform and educate the general public, policy makers, land managers and other scientists of the importance and global significance of soil. This is particularly true for soil biology and biodiversity.



To many people soil appears as solid ground. However, all soils contain space for life, from pores and cracks to burrows and root systems. (EM)

Life within the soil is hidden and, therefore, often suffers from being 'out of sight, out of mind'. However, this atlas aims to raise awareness of the important roles that the soil biota play in driving life on Earth, and demonstrate that soil is a vital habitat that needs to be managed in a sustainable way or, in some cases, protected from misuse and degradational processes.

A key goal of this atlas is to provide non-specialists with access to information about this unseen world through a comprehensive guide to the belowground environment, the organisms that live there and the functions carried out by soil biota in general.

In order to better explain the complex interactions that occur among organisms in the soil, this atlas is divided into six main sections.

Organism size	Group	Known species	Estimated species	% described
	Vascular plants	350 700	400 000	88 %
	Macrofauna			
	Earthworms	7 000*	30 000*	23 %
	Ants	14 000	25 000 - 30 000	60 - 50 %
	Termites	2 700	3 100	87 %
	Mesofauna			
	Mites	40 000*	100 000	55 %
	Collembolans	8 500*	50 000	17 %
	Microfauna ad microorganisms			
	Nematodes	20 000 - 25 000*	1 000 000 - 10 000 000*	0.2 - 2.5 %
	Protists	21 000*	7 000 000 - 70 000 000*	0.03 - 0.3 %
	Fungi	97 000	1 500 000 - 5 100 000	1.9 - 6.5 %
	Bacteria	15 000	>1 000 000	< 1.5 %

Known and estimated number of species of soil organisms and vascular plants organised according to size. Values of estimated diversity comply with the published literature, and are supported by expert judgement. Asterisks indicate numbers of species that live in the soil (updated from Barrios, Ecological Economics, 2007). [1,2]

The first section aims to provide an overview of the factors that determine the main characteristics of the habitat by describing the key soil-forming factors and how soils vary on a global scale, while the second section presents a visual introduction to, and description of, the main groups of soil organisms. Given the astonishing levels of variation of life present in soils, it is impossible to present a complete overview of all soil biodiversity in this publication (just listing all of the known species of bacteria found in soils could take up many hundreds of pages). Starting with the smallest organisms, namely bacteria, and working up through the taxonomic groups, from fungi and nematodes to the insects and mammals that we are more familiar with, this section gives a taste of the breadth of different types of organisms which live, usually unnoticed, beneath our feet.

The third section describes the patterns of soil biodiversity from micro to global scales, both geographically by specific ecosystems and in time. The fourth, fifth and sixth sections are linked in explaining how soil biota drive ecosystem services; how ecosystem services are under threat from a range of pressures, such as land use and climate change, and what measures may be taken to protect soil organisms and the benefits they provide to society.

The final section outlines a series of policy, education and outreach initiatives to support soil biodiversity management and conservation. The atlas also contains a supporting glossary and suggestions for further reading.

The atlas is an activity of the Global Soil Biodiversity Initiative, which was launched in September 2011 to develop a coherent platform for promoting the translation of expert knowledge of soil biodiversity into environmental policy and sustainable land management for the protection and enhancement of ecosystem services (see Chapter IV).

A fungus emerges from the soil. The soil that lies beneath our feet is teeming with life. Much of it unknown and beyond the comprehension of most. Soil is the living shell of planet Earth. (WJ)

The Global Soil Biodiversity Atlas was targeted as a contribution to the International Year of Soils 2015 and is a follow up to the highly acclaimed European Atlas of Soil Biodiversity, which was published by the European Commission as a contribution to the 2010 International Year of Biodiversity. By providing a global perspective on soil biodiversity and related issues, the atlas discusses the steps being taken to increase our appreciation of soil biodiversity and the development of measures to protect this vital resource.

Stable, healthy and productive landscapes reflect underpinning soil characteristics (Ngorongoro Conservation Area in Tanzania, East Africa). (VL)

Soil is alive!

- According to the United Nations Convention on Biological Diversity (CBD), biodiversity is defined as the variation of life from genes to species, communities, ecosystems and landscapes.
- While there is no formal unit of biodiversity, the expression is used to represent the totality of life through taxonomic, ecological, morphological and molecular diversity.
- Soil biodiversity reflects the mix of living organisms in the soil. These organisms interact with one another and with plants and small animals, thus forming a web of biological activity.
- Soil biodiversity varies greatly across the globe as the species numbers, composition and diversity of a given soil depend on factors such as air, temperature, acidity, moisture, nutrient content and organic matter.
- Soils are conditioned by climate, altitude, soil parent material, land use and the presence of living organisms (especially humans).
- Soils provide an amazing habitat and may contain more than 10 000 species per square metre.
- A single gramme of soil may contain millions of individual cells and thousands of species of bacteria. Bacterial biomass can amount to 1 - 2 tonnes per hectare in temperate grasslands.
- Soil organisms maintain critical processes, such as carbon storage, nutrient cycling and plant species diversity, and play a key role in maintaining soil fertility.
- Earthworms, termites and other soil organisms enhance soil productivity by mixing the upper soil layers, which redistributes nutrients, aerates the soil and increases surface water infiltration. Earthworms increase crop yields by 25 %, on average.

What is soil?

The term 'soil' means different things to different people. To the vast majority living in cities, soil is simply the 'dirt' or 'dust' to be cleaned from their hands or the vegetables that they buy to eat. However, to the majority of gardeners or farmers, soil is the uppermost surface of the Earth that is cultivated and nurtured to produce crops. To the engineer, it is the 'overburden' or the unwanted loose material that needs to be removed to provide a more stable foundation upon which to build. To the climate change modeller, it is both a storehouse and source of carbon and greenhouse gasses, such as methane, carbon dioxide and nitrous oxide. To the hydrologist, soil is a buffer that stores rain, thus alleviating floods and providing drinking water as well as base flow for rivers. Finally, to the biologist, it is a fascinating habitat teeming with life.

In fact, soil is all of these things. Soil is the living, breathing skin of our planet. Soil is the result of the interactions between the atmosphere (as governed by climate), the biosphere (local vegetation, animal activities, including those of humans) and the geosphere (the rocks and sediments that form the upper few metres of the Earth's solid crust). Those of us who study soil have a definition for it. We say 'soil is any loose material on the surface of the Earth that is capable of supporting life' and these life-supporting functions have been understood from the earliest of times.

'A nation that destroys its soils destroys itself.'

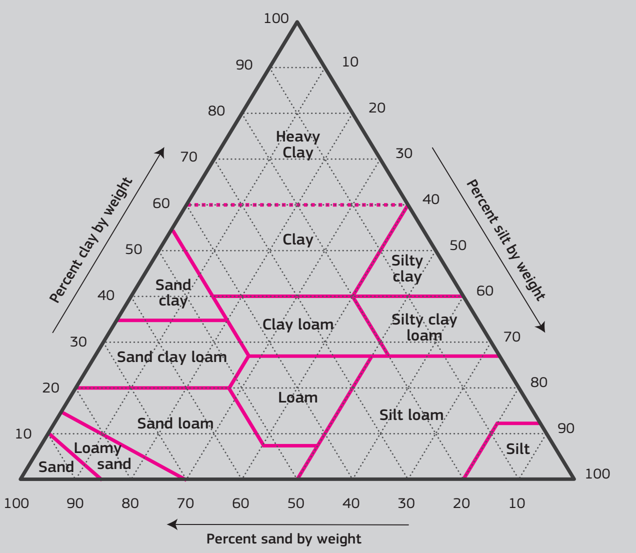
Franklin D. Roosevelt , Letter to all State Governors on a Uniform Soil Conservation Law, 1937.

What is soil made of?

All of us have come into contact with soil at some point in our lives and most people are familiar with such terms as clay, silt, sand or peat. In reality, soil consists of a mixture of non-living minerals and living organisms that represent the products of weathering and biochemical processes. Rocks are weathered into individual grains, while decaying vegetation and living organisms are referred to as soil organic matter. Pores and cracks in the soil contain air with a higher concentration of carbon dioxide than found in the atmosphere. When we handle soil, the fact that it usually stains and moistens our fingers shows that it holds different amounts of water, organic compounds and minerals.

The look and feel of soils

- The physical appearance of soils is described by two characteristics known as texture and structure. Both are strongly related to the parent material of the soil. [3]
- Texture describes the size and type of mineral particles that make up the soil and are characterised according to their diameter. They range from gravel (> 2 mm), sand (2.0-0.063 mm), silt (0.63-0.02 mm) to clay (< 0.002 mm). Texture can be estimated by rubbing soil between your fingers. Clay soils will feel smooth while sandy soils are gritty.
- Sand particles are large, drain easily, and have limited ability to retain moisture and minimal chemical activity. By contrast, clay particles are very small but with a large surface area, can retain moisture, are very chemically active and have a higher nutrient content.
- Structure refers to the arrangement of these soil particles into larger aggregates, or clumps, of different sizes and shapes and the pore spaces that are left between them. It is into these spaces that root hairs grow and from which they extract water and oxygen.



Soil texture triangle – most soils tend to be a combination of sand, silt and clay. Soils are often referred to by their texture class. Therefore, a soil with 40 % sand, 40 % silt and 20 % clay is a loam, while another soil with 10 % sand, 30 % silt and 70 % clay is referred to as a heavy clay. (FAO)

The soil in profile

In most cases, if we dig a hole into the ground and look at the vertical section of soil that is revealed, we will notice a number of different layers, roughly parallel to the surface. These layers are referred to as 'horizons' and are the result of a range of geological, chemical and biological processes that have acted upon the parent material over the lifetime of the soil (see pages 20-25). Relatively young soils, such as those on river sediments, sand dunes or volcanic ash, may have indistinct or even no horizon formation. As age increases, horizons tend to be more apparent (there are exceptions, such as in deeply weathered tropical or permafrost-affected soils).

Most soils usually exhibit three or four horizons (there can be more or less). Horizons are generally described by their colour, texture, structure, organic matter and the presence of carbonates. More detailed characteristics can be measured in the laboratory. Some soils show a gradual change from one horizon to another, while other soils may possess horizons that have markedly different characteristics to each other.

The identification and quantitative description of horizons are important aspects of studying soils. Most soils conform to a similar general pattern of horizons and in soil science, major horizons are usually denoted by a capital letter as a means of shorthand and easy communication (typically followed by several alphanumerical characters to denote a characteristic feature). [3]

Know your A, B, C...

When a vertical section of the soil is examined, the thin uppermost layer normally contains the undecomposed or slightly decomposed remains of plants lying on the surface of the soil. This layer is called an organic horizon and is referred to by the letter 'O'. The O horizon is not saturated by water for prolonged periods and its mineral content is very low. Where the accumulations of organic material on the soil's surface are saturated by water for prolonged periods, this is referred to as an H horizon. Organic matter in both the H and O horizons may be further divided into the following: 1) slightly decomposed – plant remains are visible to the naked eye; 2) an intermediate phase where decomposition is more advanced but plant remains are still visible; 3) a completely decomposed organic layer on top of the mineral soil.

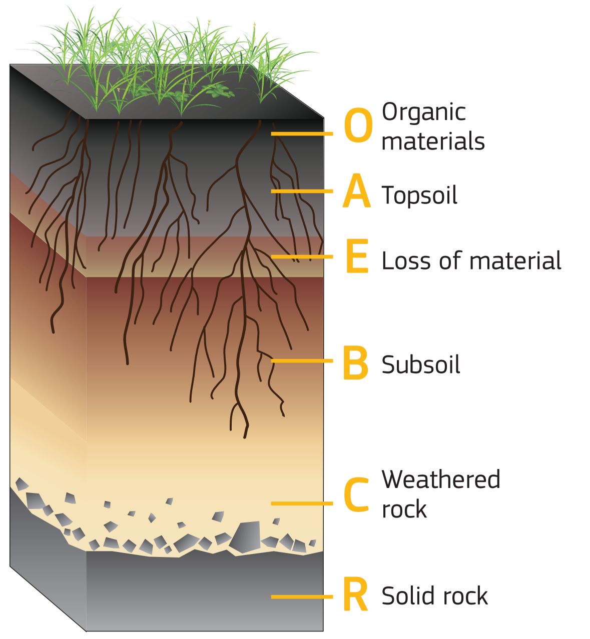
Beneath the O horizon, a dark horizon containing a mixture of organic and mineral material can be recognised, which is referred to by the letter 'A'. The A horizon is the topsoil, which contains most of the organic material within the soil, hence its darker colour. It is the engine room of the soil where most of its biological and chemical activities occur (e.g. biomass growth, dead litter and root decay and release of nutrients, formation of organic acids and their reactions with minerals, etc.). If the topsoil layer is removed by erosion or human activity, most of the soil's ecological potential goes with it. While the topsoil layer will regenerate over time, if left undisturbed it may take hundreds of years for its full original potential to be restored.

Below the topsoil (O and A horizons) lies the mineral subsoil containing one or more brighter coloured layers that are referred to by the letter 'B'. In most soils, the B horizon contains much less organic material than topsoil (often making it lighter in colour); however, this horizon is still exploited by plant roots and soil organisms that use the stored water, air and nutrients.

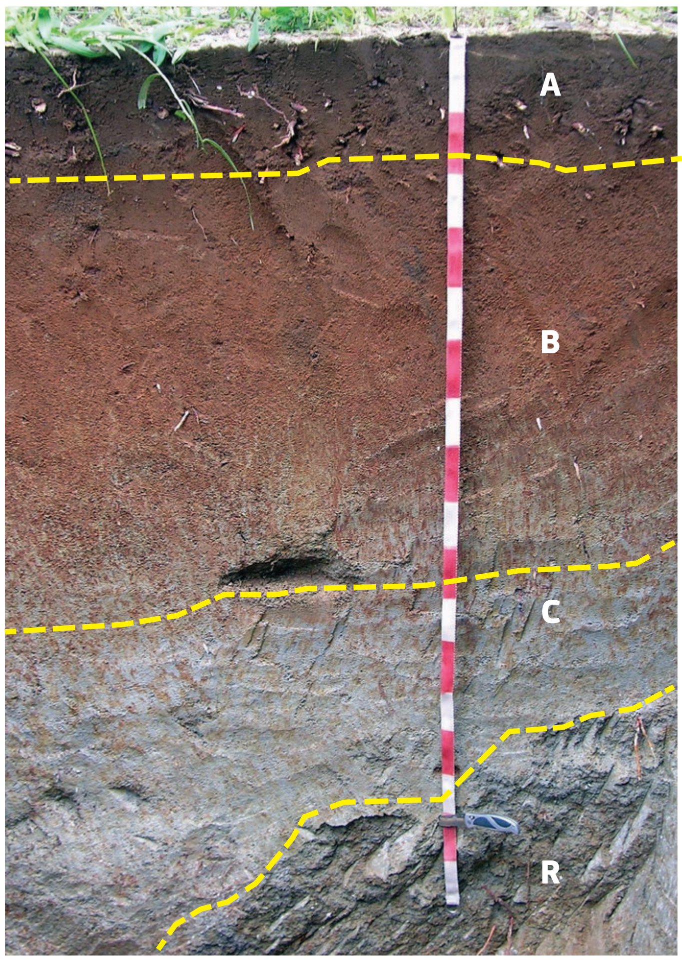
Brownish, yellowish or reddish soil colours originate from oxides (very often iron) formed by the weathering of minerals, whereas greyish or bluish tones can result from chemical reactions in waterlogged conditions. Toward the base of the subsoil, the soil structure gradually becomes less apparent as the factors affecting its development decrease in influence.

Eventually, a layer is reached where the influence of soil-forming processes is less apparent. This layer is referred to by the letter 'C'. This horizon lies above hard bedrock or parent material. The characteristics are usually very different to the A and B horizons and may contain weathered blocks of the underlying geological substrate. The 'R' horizon basically denotes the layer of hard bedrock underneath the soil. Soils formed *in situ* will exhibit strong similarities to this layer.

Soils formed predominantly from the decaying remains of plants are referred to as peat and do not reflect the standard A-B-C arrangements of mineral soils. Horizons in organic soil tend to reflect the degree of decomposition or inputs of mineral material.



A hypothetical soil profile showing the main horizons in a typical mineral soil and their relation to parent material, root development and soil-forming processes. The E horizon occurs in soils when materials such as clay, iron and aluminium have been destroyed or flushed to deeper layers by percolating water. E horizons are usually lighter in colour (but not always) and have a coarser texture. Other possible horizon codes are L (sediments deposited in a body of water) and W (presence of water layers). (LJ)



A classic A-B-C-R soil horizon sequence under arable cultivation in Tanzania. The greyish, soft C horizon has weathered from the hard bedrock below (R), and provided the parent material for the development of the A and B horizons. The uppermost, dark A horizon (0-20 cm) indicates a higher level of organic matter. Below is a well structured, reddish B horizon (20-100 cm) with large amounts of iron oxides and clay, as a result of weathering and soil-forming processes. Plant roots and burrows are clearly visible in both the A and B horizons. (EM, JRC, LJ)

Soil – it's amazing!

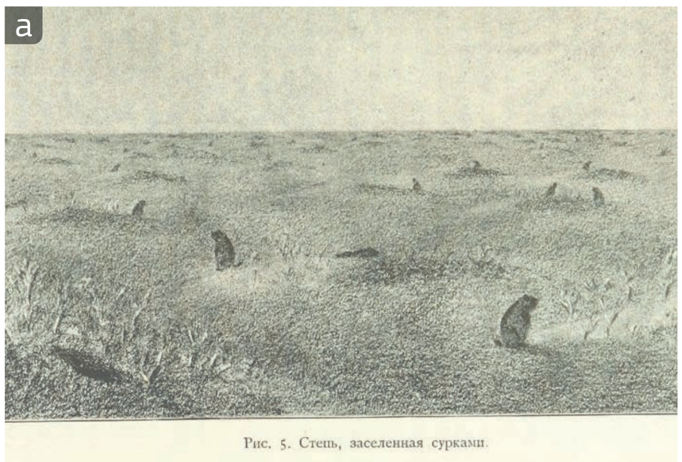
- Soil makes up the outermost layer of our planet, while topsoil is the most productive and biologically active soil layer.
- A typical mineral soil sample is 45 % minerals, 25 % water, 25 % air and 5 % organic matter.
- Soil has varying amounts of organic matter (living and dead organisms). It is estimated that 5-10 tonnes of animal life can be found in one hectare of temperate grassland soil.
- Ten tonnes of topsoil spread over one hectare is only a few mm thick, but it can take more than 500 years to form 2 cm of topsoil.
- Soils are generally around 1-2 m deep. However, some soils are very shallow (just a few centimetres) while soils found on old, stable land surfaces are much, much deeper. The Phillipi Peatland in Greece is reputed to be 190 m deep.
- New soil material is continuously deposited by rivers, volcanoes and wind on the Earth's surface. While soils in glaciated regions are relatively young, older, more weathered soils can be found closer to the tropics. The three thousand million year old Nsuze Paleosol in South Africa is the world's oldest soil deposit.

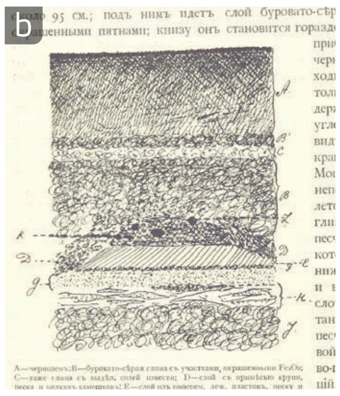
Where do soils come from?

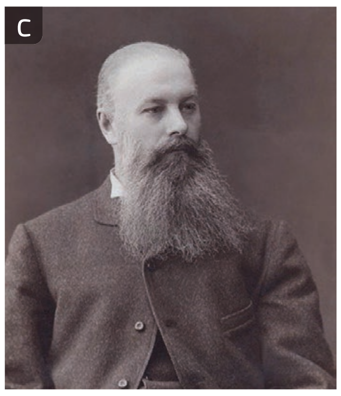
Soil-forming factors

As can be seen from the pictures on this page, the appearance and characteristics of soils can vary considerably from place to place. The next few pages of the atlas will outline the main soil-forming factors and illustrate how they dictate the properties of a particular soil.

The Russian scientist Vasily Vasilievich Dokuchaev is commonly regarded as the father of pedology, the scientific discipline concerned with all aspects of soils. He was the first person to articulate that geographical variations in soil characteristics were related to climatic, topographic conditions, time and vegetation as well as geological factors (parent material). His ideas were further developed by a number of soil scientists, including Hans Jenny who, in 1941 [4], established a mathematical relationship that states that the observed properties of soil are the result of the interaction of many variables, the most important of which are: parent material, topography or position in the landscape, climate, living organisms/soil biodiversity, human activities and time (see following pages). According to this relationship, variations in living communities, parent material, climate or the age of the soil will result in specific soil characteristics.







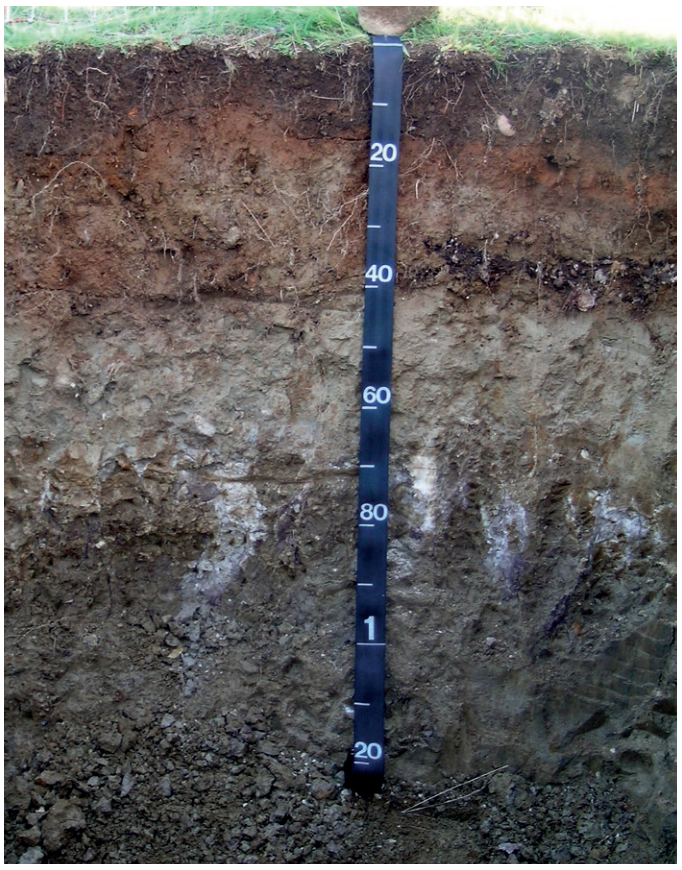
In his books (**a–b**), Vasily Vasilievich Dokuchaev (**c**), the father of pedology, was the first to present the factors influencing soil formation. (TBL, IV)

For example, the weathering of solid bedrock through processes such as heating-cooling or freeze-thaw cycles (determined by topography and climate) produces a matrix of rock fragments (also known as regolith). Furthermore, weathering leads to the production of finer structures containing crystalline minerals that have been liberated from the rock. These fine-textured materials provide ideal conditions for seeds to germinate and lichens, mosses and higher plants to become established. The growth of vegetation is supported by the decomposition of minerals into simple molecules or compounds that act as plant nutrients. As plants become established, dead leaves will fall on the surface and decay to form thin organic layers, which in turn, support the next cycle of plant growth by returning the nutrients to the soil. Over time, the parent material is buried by more and more organic matter, thus allowing larger plants to grow. The slope or aspect of the site may determine growing conditions, but also the drainage and inputs or removal of materials. In this way, a soil will form with characteristics that reflect the interplay among the various factors.

A changing climate may reduce the weathering processes and, consequently, halt the supply of parent material and the release of minerals. Alternatively, climate change may favour a more luxuriant vegetation community, leading to the production of more plant matter, and resulting in deeper organic layers. In both cases, the soil characteristics will be different from the initial example.

Much more information on soil-forming processes can be found in most general soil text books (see pages 172-173).

This photograph from Africa shows a deep, coarse-textured, iron-rich soil that has developed under a tropical climate. The darker band just below the surface (0-20 cm) is the result of ploughing. (VL)



This profile from North America shows a stratified soil that has developed on volcanic material (ash and ejecta). The different colours reflect the weathering of minerals (predominantly iron and aluminium oxides) and can contain significant amounts of volcanic glass. The uppermost 15 cm shows a dark, organic-rich horizon. Such soils are typically very fertile and can usually support intensive cropping or forests. (EM)

This soil from Europe is characterised by a surface layer (0-50 cm) rich in humus and calcium ions bound to soil particles. This gives a well-aggregated structure and supports abundant natural grass vegetation. Such soils occur in climates with an annual and seasonal rainfall of 450-600 mm, cold winters and relatively short, hot summers (e.g. North American prairies, Eurasian steppes). In colder areas, the surface horizon can be as much as two metres deep. Due to the low rainfall, lime is not leached from these soils, making them some of the most naturally fertile soils on the planet. (EM)

A fine-textured soil from Australia with high levels of swelling and shrinking clay minerals. Initially derived from the weathering of basic rocks, such as basalt, the clays were later redeposited in still water conditions. The dark colour indicates that iron is virtually absent from this soil. Note the cracks and smooth surfaces of sheer planes, which are evidence of churning within the soil as a result of shrinking and swelling in wet and dry conditions. (SD)

This fine-textured soil from the Russian Arctic is characterised by distorted and homogenised horizons as a result of cryoturbation – the mixing of a soil due to alternating thawing and freezing cycles. Such soils are typical of very cold climates with permafrost. The dark colour in the profile is patches of organic matter that has been dragged from the surface into the soil profile. Consequently, these soils are very important in the global carbon cycle and climate change assessments. (SG)

A shallow, stony soil from South America overlaying hard rock, reflecting very recent soil formation. This is the most widespread soil type on the planet; such soils are particularly common in mountain areas, notably in Asia, South America, northern Canada, Alaska and in the Saharan and Arabian deserts. However, they are unsuitable for agriculture because of their inability to hold water. They are generally used for extensive grazing or to support natural woodlands. (JN)

Soil-forming factors – Parent material

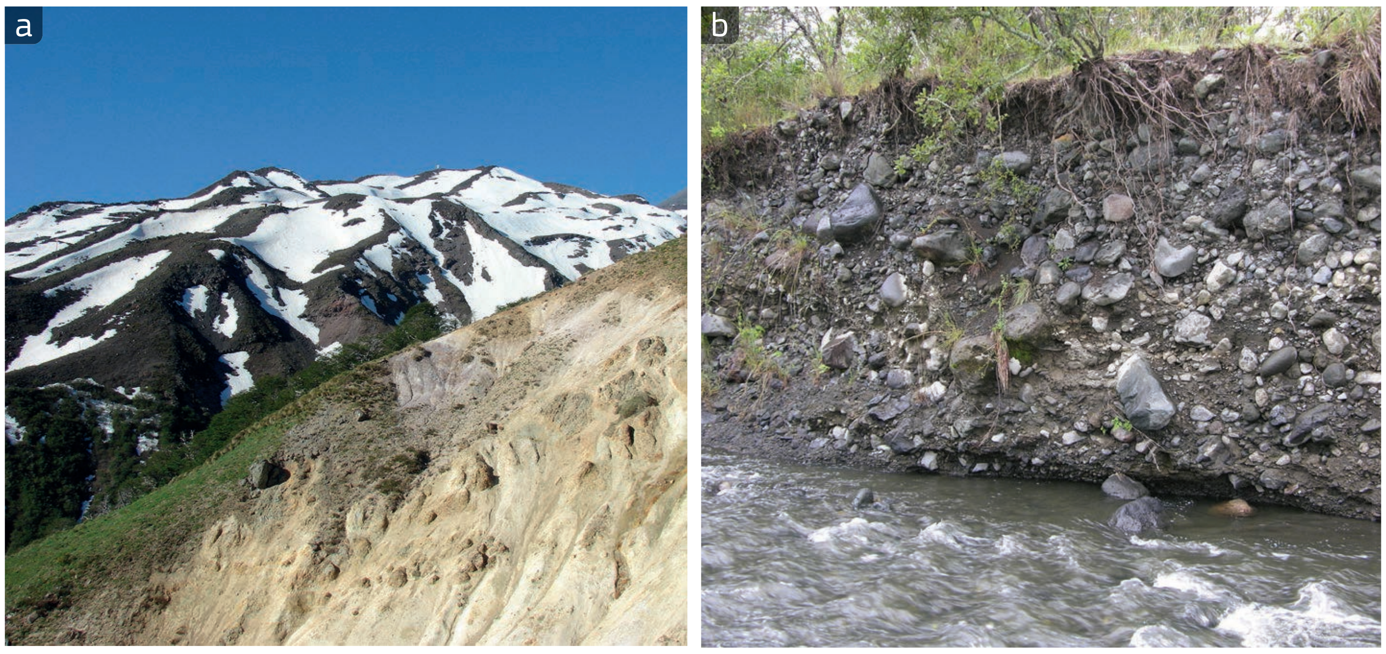
Parent material refers to the substance from which the soil has been derived. While in most cases it is of geological origin, parent material can also be organic. The nature of the parent material can have a profound influence on the characteristics of the soil. For example, the texture of sandy soils is determined largely by the presence of quartz grains in the parent material, which, in turn, controls the movement of water through the soil. The mineralogy of the parent material is mirrored in the soil and can determine the weathering process and control the natural vegetation composition. For example, lime-rich soils are generally derived from calcareous rocks (e.g. limestone and chalk) or sediments derived from such deposits. In turn, lime-rich soils can offset the development of acidic conditions but may not support organisms and plants that are not tolerant of alkaline soil conditions (e.g. rhododendrons).

Three types of parent material are recognised: 1) unconsolidated deposits that have been transported by ice, water, wind or gravity; 2) weathered materials directly overlying consolidated hard rock from which they originate; 3) organic material composed of decaying or partially decayed plant remains. In the former two cases, the parent material can be weathered through physical destruction of rock (freezing or drying cycles) or chemical reactions (dissolution of elements). Weathered parent material is often referred to as saprolite.

While the forces created by the expansion and contraction of minerals, induced by daily temperature variations, cause rocks to shatter and exfoliate (especially in hot deserts), in most cases water is the dominant agent in weathering processes. Water can cause rocks to shatter through repeated freezing and thawing of water trapped in rock cavities. Water also initiates solution and hydrolysis (the destruction of a compound through a reaction with water that produces an acid and a base) that liberate minerals contained within the rock. Water also supports life which, in certain situations, is a major contributor to the weathering process. Plant roots can cause physical weathering as they grow and expand inside cracks in the rocks. Roots and decaying vegetation also produce organic compounds such as solvents, acids and alkalines that enhance the actions of percolating rainwater.

The degree of weathering depends on a number of environmental factors, such as temperature (determined by climate, exposure and altitude), the rate of water percolation (determined by texture, relief, climate), the presence of oxygen (again texture and climate), the surface area of the parent material (largely determined by the geological structure) and the mineralogy of the parent material (for example, quartz is much more stable than olivine). Weathering of minerals continues in the soil following a sequence from the least to the most stable minerals. Minerals undergo changes that cause the formation of secondary minerals and other compounds that are soluble in water (to varying degrees).

Soil is considered organic if it contains more than 20 % of organic matter. By contrast, mineral soils contain less than 20 % organic matter but can possess organic surface horizons.



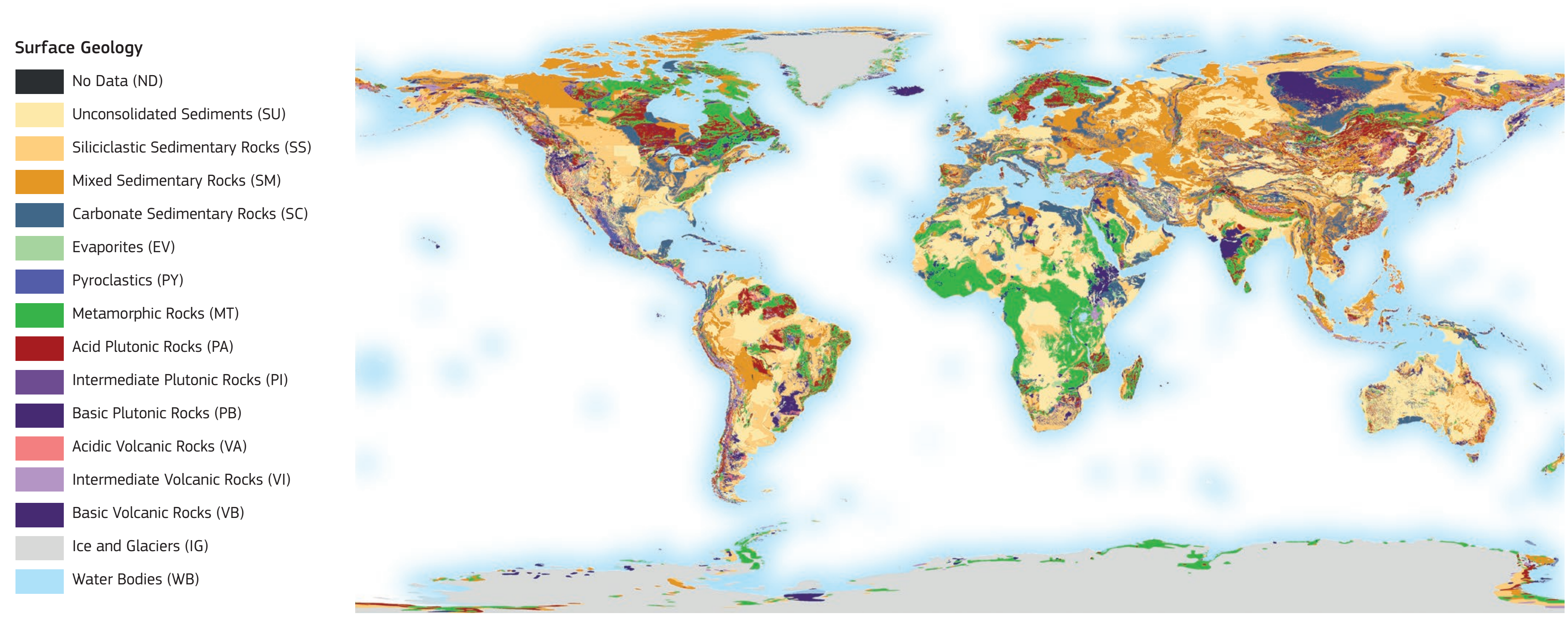
Examples of soil formation on continuous (**a**) hard bedrock in Chile and (**b**) transported sediments in East Africa, in this case, of fluvial origin. Where consolidated parent material lies close to the surface, soil depth is generally shallow and horizon development is weak. Unconsolidated sediments can completely mask the characteristics of the underlying bedrock. (MF, EM)

An example of a soil that has developed on organic parent material. Such soils are known as peat and develop when the decay of plant material is suppressed due to lack of oxygen in waterlogged conditions (anaerobic), such as those found in bogs, fens, moors, mires or swamps, or due to low temperatures (e.g. the tundra). Three main types of peat are recognised: sapric (very decomposed, hardly any recognisable plant fibres), hemic (moderately decomposed) and fibric (slightly decomposed). Organic soils generally accumulate very slowly. (EM)

What is a rock?

- A rock is a naturally occurring solid material with a distinctive mineral composition. There are three basic types of rock: igneous, sedimentary and metamorphic.
- Igneous rocks form from molten material. They include rocks, such as basalt, that are ejected from volcanoes and granite, which is formed by magma that solidifies far underground. They are generally categorised by the size of their crystals and the presence of the mineral quartz.
- Sedimentary rocks are formed by the deposition of weathered rock fragments by wind or water. Shales are deposited on ocean floors. Conglomerates and sandstones are resistant fragments of other rocks deposited by rivers, while limestone and chalk are created through the precipitation of calcium carbonate in oceans. Fossils are found in sedimentary rocks.
- Metamorphic rocks are igneous or sedimentary rocks that have been transformed by intense heat, pressure or the intrusion of fluids resulting in changes in mineralogy and structure. Examples include marble (from limestone), slate (from shale) and gneiss (from granite).

The map below shows lithology – the geological character of the Earth's surface in terms of origin and mineral characteristics of rock outcrops and more recent deposits. This makes it a good proxy for soil parent material. While the term volcanic is probably widely understood, pyroclastics are the products of explosive volcanic eruptions, whereas plutonic indicates molten rock that cooled underground (see box on page 22 for definition of acid, basic and intermediate rocks). Unconsolidated sediments include alluvium (deposited by water), aeolian (deposited by wind), organic (peat deposits) and colluvium (transported by gravity). Saline sediments (EV) reflect the evaporation of lakes. Siliciclastic sedimentary rocks contain high levels of the mineral quartz (e.g. sandstones) while carbonates denote limestone and chalk. Metamorphic indicates that the original chemistry and structure have been altered by heat or pressure (e.g. limestone to marble, mudstone to slate and granite to gneiss). The map shows that most soils have developed on unconsolidated sediments and sedimentary rocks. It should be noted that the general nature of this map means that at a local level, the conditions may be quite different to that shown. (JH, NM) [5]



Soil-forming factors – Topography

The shape of the land surface, also referred to as relief or topography, is a key soil-forming factor as it has an important influence on local climate, vegetation and the movement of water. Mountains can affect the amount and intensity of precipitation and vegetation growth on a large scale; whereas locally, the angle or slope of the ground controls drainage and movement of materials. Even small variations in elevation can be important in flat lands. River terraces or small depressions can lead to localised improved drainage or waterlogging, respectively. Micro-topography can be particularly important if saline groundwater occurs close to the surface as it will affect evaporation rates.

The position of soil in the landscape is very important. Generally, soils found at the top of a slope tend to be freely draining, while those at the foot of a slope or on the floor of a valley are often poorly drained. In some cases, the water table may be near to or at the surface. In this case, different soils may form on the same parent material, under the same climate and even vegetation type (e.g. a grass-covered slope). Soils occurring on the middle of slopes receive sediment and solutions from higher up but, at the same time, lose material to soils below. In these cases, the actual shape of the slope is important as smooth, irregular, convex or concave slopes will result in different soil characteristics.

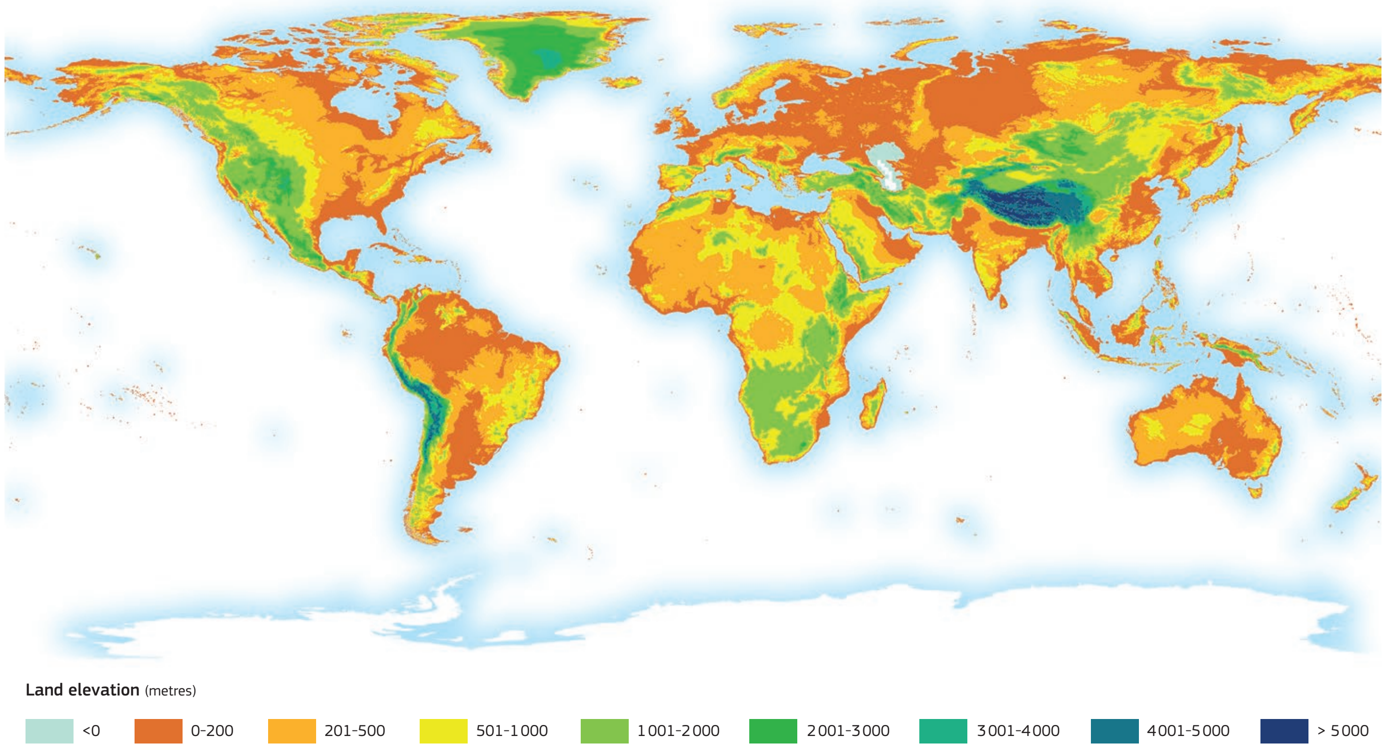
The map on the right shows the variation in elevation of the land surface in metres above sea level. The map is based on measurements taken by a specially modified radar sensor carried on board the NASA Space Shuttle as it orbited the planet [6].

The light turquoise and dark orange colours represent areas below or just above sea level, respectively. The low-lying salt lakes of North Africa, the Caspian Sea and the Dutch coast are particularly evident. In fact, the lowest point in the world is the Dead Sea on the Israel-Jordan border, which is 411 metres below sea level.

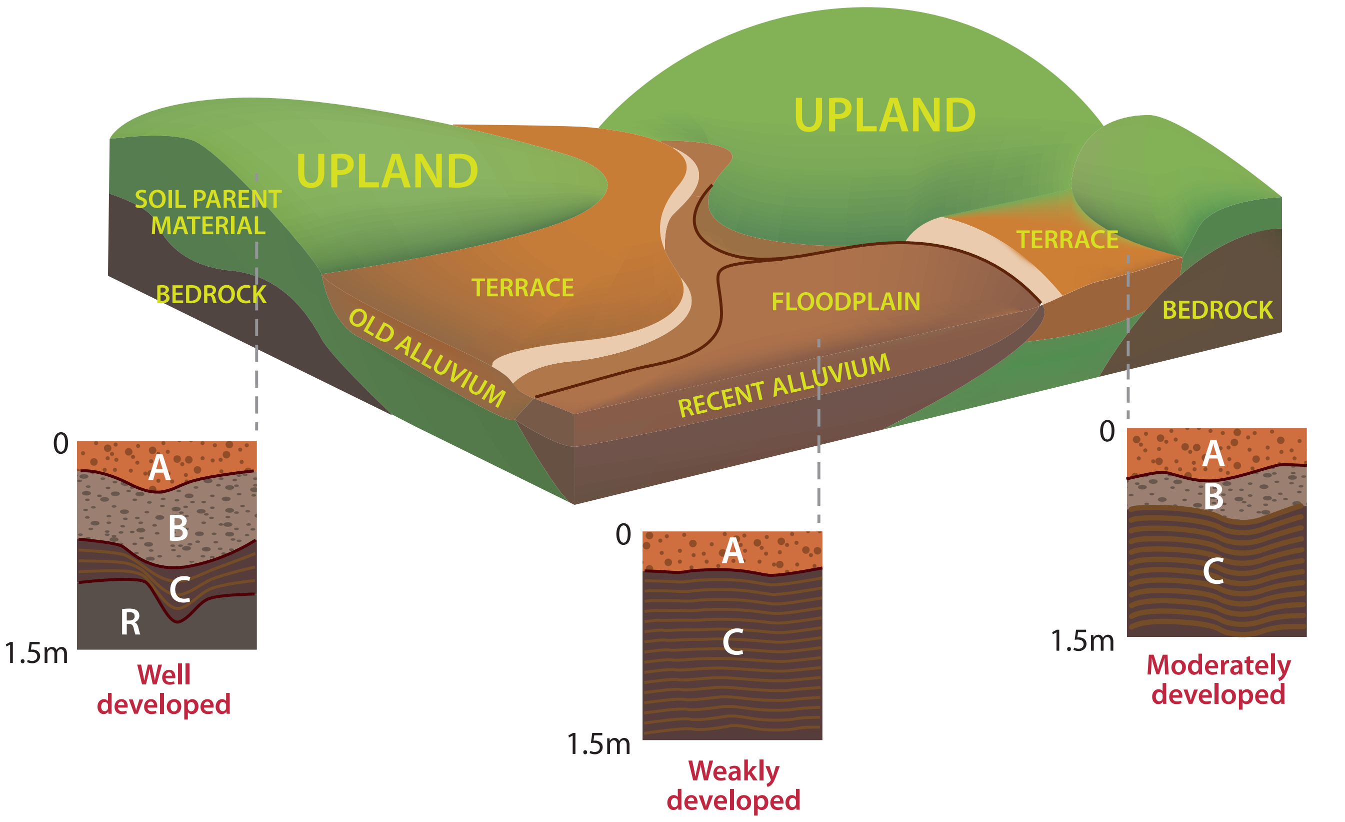
The dark orange areas show the extent of landscapes with low elevation and relief. These include the wetlands of Siberia, much of northern and central Eurasia, the Amazon and Paraná-Paraguay Basins in South America and the coastal lands around the Gulf of Mexico and Hudson Bay, which are generally flat or only gently undulating. Light orange denotes the high plains where the landscape will begin to show evidence of soil erosion on steeper slopes (eastern and central North America, northern Africa and large parts of Australia).

The yellow colours represent upland regions which, in some places, give way to mountainous areas (green). The Rocky Mountain Range, Greenland, the Alps, the Atlas Mountains of North Africa, the Anatolian Plateau and Zagros Mountains in the Middle East, the Southern Highlands in Tanzania and Mongolia are clearly visible. The highest elevations on the planet (dark blue) are found in the Himalayas where Mount Everest reaches a height of 8 848 metres above sea level. High mountain peaks are also present in the South American Andes (Mount Aconcagua, 6 962 m).

In addition to drainage, rainfall and solar radiation, another key factor for soil formation is temperature. While modified by latitude, proximity to the sea and some meteorological conditions known as inversions, ambient temperature generally drops with increasing elevation. This reduction in temperature is known as the lapse rate and, as a rule, temperature drops between 5 and 10 °C/1 000 m depending on air humidity (under normal atmospheric conditions, a value of 6.4 °C/1 000 m is usually quoted).



Map showing the elevation of land around the world. The darker green and blue colours represent areas of higher elevation, while the yellow and orange areas are below 1 000 m. (LJ) [6]



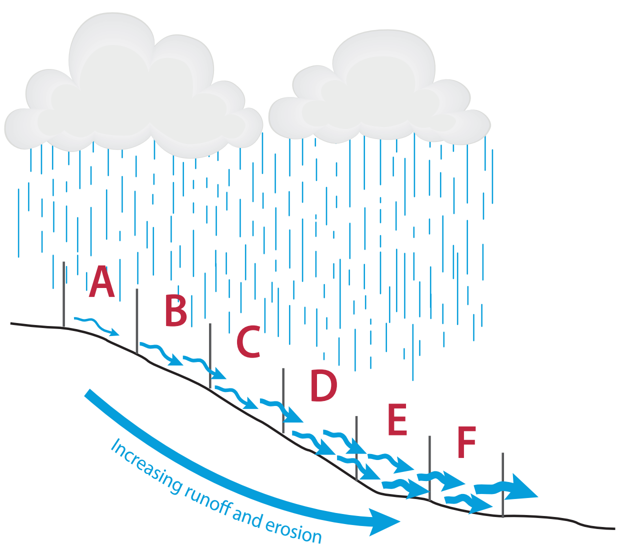
The position of a soil in the landscape is important in determining its characteristics. The graphic illustrates the conceptual differences in the development of the soil profile according to a specific topographic setting (UM, TC).

Soils on sloping ground – the Catena

- Catena comes from the Latin word for chain and describes the sequence of soils down a slope.
- On sloping ground with consistent parent material, the influence of relief dominates other soil-forming factors.
- The theory of the catena originates from a soil reconnaissance survey that was carried out by an agricultural officer, Geoffrey Milne, in what is now Tanzania during 1935-1936.
- He realised that the soils running from the crest of a hill to the floor of the swamp in the valley below it differed somewhat from its neighbours and that the same soil types were occurring in the same landscape setting. This accelerated the production of soil maps.
- Interestingly, local farmers had an indigenous yet sophisticated understanding of the role of topography in determining soil characteristics.
- Milne's initial ideas were set out in a ground-breaking paper that was published in 1947 [7]. He became one of the outstanding figures in international soil science and his concept provided the foundation for soil surveying all over the world.

The photograph shows a very weathered granite outcrop in Sukumaland, Tanzania, that is the uppermost ridge section of the original catena sequence described by Milne in 1936. On the upper part of the slope, adjacent to the rock outcrop, sandy soils reflect the weathering of the granite. Down the slope, increasing clay content gives rise to sandy-clay soils and eventually seasonally waterlogged soils with a marked difference in texture between the topsoil and subsoil (see page 27: Planosols). As the slope lessens, salt-affected or lime-rich soils develop, which grade into heavy clay soils that shrink and swell according to their moisture content. Soil erosion exposes iron-rich clay nodules that harden irreversibly when exposed to air and sunlight (see page 26). (JD)

Soils occurring at the foot of slopes receive greater amounts of water and sediment compared to those on higher ground. While erosion is considered a threat to soil functions, it can also be regarded as a soil-forming process by depositing new parent material at the foot of slopes. However, soil at location A will probably be well drained while at location F, waterlogging or saturated ground may be common. (JRC, LJ)



Soil-forming factors – Climate

Climatic zones

Soil formation depends enormously on the climate as temperature and moisture levels affect weathering processes and biological activity. Where precipitation exceeds evapotranspiration, leaching or saturated soils can occur. When the opposite is true, salts can rise to the surface. Chemical weathering is very active in areas with high temperatures and high humidity, while physical weathering dominates in hot, dry desert regions.

About 36 % of the Earth's land surface is located within the Tropical Belt, where temperatures are warm all year round (generally 25 - 28 °C) and lack extreme seasons. In countries south of the Equator, the seasons are the opposite to the countries that lie north of the Equator. The broad climatic patterns are driven by ocean currents, weather systems, distance from the sea and topography (mountain chains often act as climatic barriers). The following five main climatic groups can be distinguished:

(A) Tropical: characterised by constant high temperatures, with all 12 months of the year having an average temperature of 18 °C or higher, with little or no seasonality. It is subdivided into tropical rainforest climate (Af) where all months have an average precipitation of at least 60 mm, and generally occurs within 5 - 10° latitude of the Equator, tropical monsoon (Am), tropical wet and dry or savannah (Aw). Sometimes As is used in place of Aw if the dry season occurs during the time of higher sun and longer days.

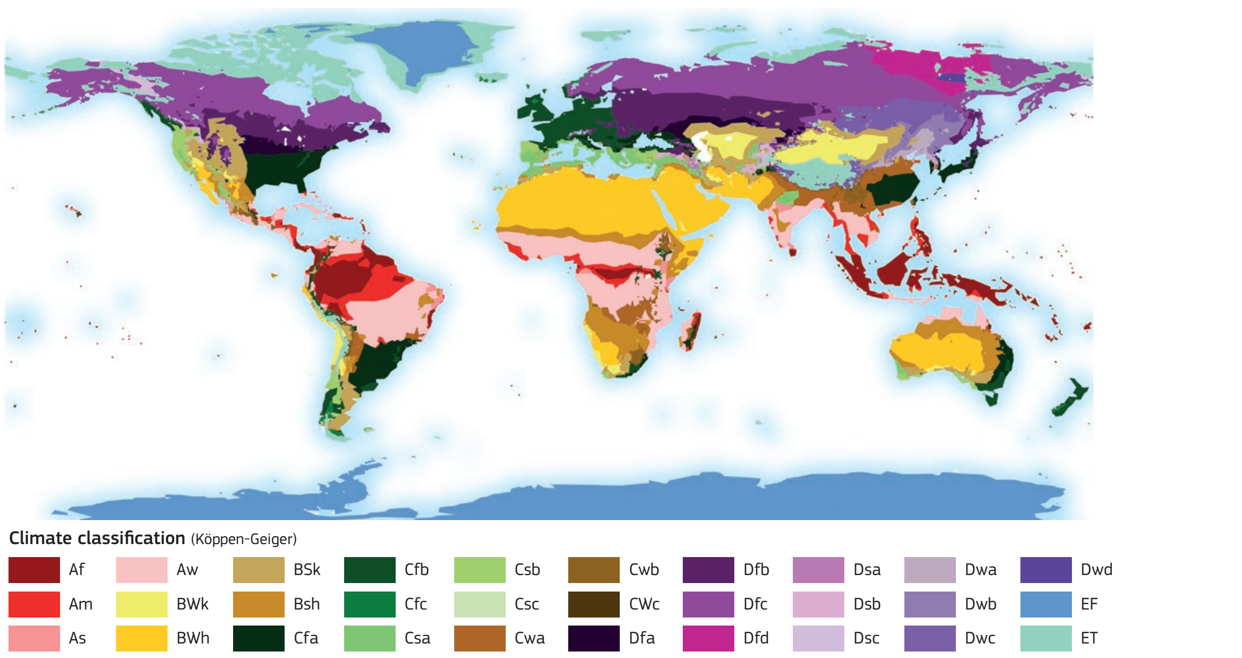
(B) Dry (arid and semiarid): where actual precipitation is less than a threshold value equal to the potential evapotranspiration. Subdivided into desert (BW) when the annual precipitation is less than 50 % of this threshold and steppe (BS) if in the range of 50 - 100 %. A third letter (*h*, *k* or *n*) can be included to indicate temperature characteristics (see map legend at top right). Additionally, a fourth letter can be specified to indicate if either the winter or summer is 'wetter' than the other half of the year.

(C) Temperate: characterised by an average temperature above 10 °C in the warmest months (April to September in the Northern Hemisphere), and a coldest month average of between −3 and 18 °C. In this group, the second letter indicates the precipitation pattern: *w* indicates dry winters, *s* indicates dry summers and *f* indicates significant precipitation in all seasons. The third letter indicates the degree of summer heat where *a* indicates that the warmest month average temperature is above 22 °C with at least four months averaging above 10 °C, *b* indicates that the warmest month averages below 22 °C, but with at least four months averaging above 10 °C, while *c* means three or fewer months have mean temperatures above 10 °C. Subdivided into dry-summer subtropical or Mediterranean (Csa/Csb), humid subtropical (Cfa, Cwa), maritime temperate or oceanic (Cfb, Cfc, Cwb, Cwc), temperate highland tropical climate with dry winters (Cwb, Cwc), maritime subarctic climates or subpolar oceanic climates (Cfc) and dry-summer maritime subalpine climates (Csc).

(D) Continental: characterised by an average temperature above 10 °C in the warmest months and a coldest month average of below −3 °C. Usually found in the interiors of continents and on east coasts north of 40° N. In the Southern Hemisphere, group D climates are extremely rare due to the smaller land masses in the middle latitudes and the almost complete absence of land at 40 - 60° S. The second and third letters are used as for group C climates, while a third letter *d* indicates three or fewer months with mean temperatures above 10 °C and a coldest month temperature of below −38 °C. Subdivided into hot summer continental climates (Dfa, Dwa, Dsa), warm summer continental or hemiboreal (Dfb, Dwb, Dsb), continental subarctic or boreal (taiga) climates (Dfc, Dwc, Dsc) and continental subarctic climates with extremely severe winters (Dfd, Dwd, Dsd).

The Tropics

- The tropics denote the area on the Earth where the sun is directly overhead at least once during the solar year. It is limited by the Tropic of Cancer, at approximately 23° 26' 16'' N, and by the Tropic of Capricorn at 23° 26' 16'' S, which marks the points where the sun is directly overhead during the summer solstice (June 21st and December 21st, respectively).
- The term 'tropical' is sometimes used in a general sense to denote a climate that is generally warm and moist all year round and where there is often lush vegetation. However, in a strict sense, a tropical climate is not arid and all months have an average temperature > 18 °C.



Map of major climatic zones according to the updated Köppen-Geiger classification scheme, based on the concept that natural vegetation is the best expression of climate (the codes of the legend are described in the adjacent text). The system combines average annual and monthly temperatures, precipitation and the seasonality of precipitation. The Earth's climate has a degree of symmetry around the Equator with warm and humid conditions dominating. Generally, these areas are flanked by hot and dry deserts. Increasing latitude, and generally altitude, in both hemispheres is marked by increasing precipitation and seasonality together with more temperate conditions. Large parts of North America and Eurasia exhibit marked continental climates, while the Arctic and Antarctic zones have low temperatures and often low precipitation. Within these zones, altitude and other localised variables produce distinctive regional climates. Climate change will have a pronounced effect on soil formation and soil biodiversity (derived from Kottek *et al.*, Meteorologische Zeitschrift, 2006). (JRC) [8]

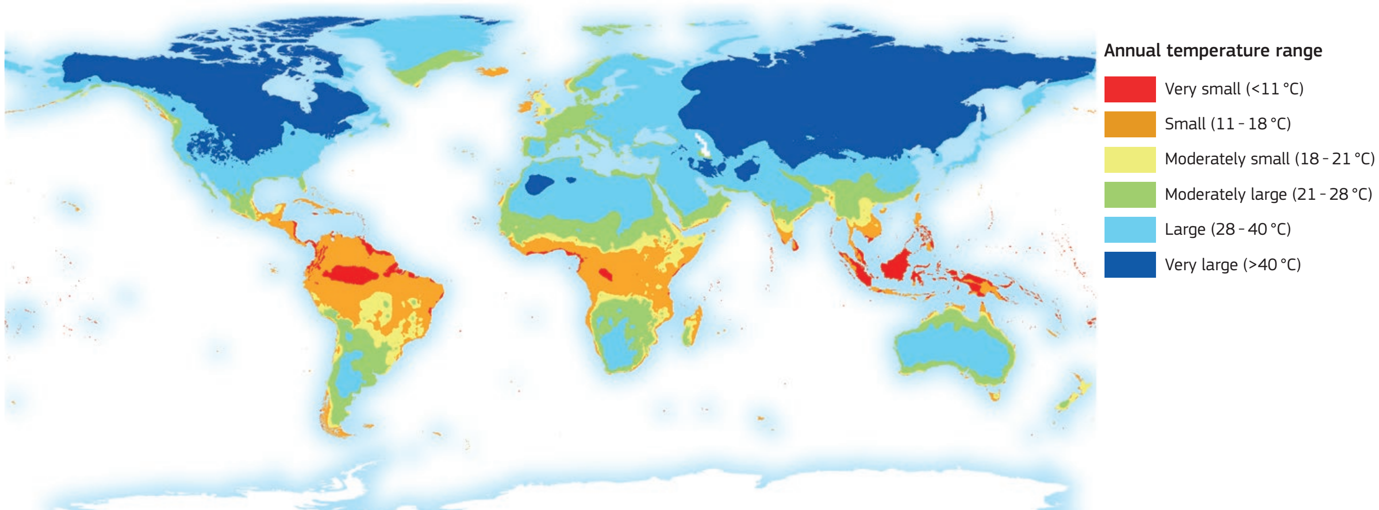
(E) Polar and alpine: characterised by average temperatures of below 10 °C throughout the year. Subdivided into tundra (ET) and ice cap (EF) where in the latter all 12 months have average temperatures below 0 °C. Occasionally, a third, lowercase letter (*w*, *s*, *f* – see group C) is added to ET climates to indicate precipitation patterns. Seasonal precipitation letters are almost never attached to EF climates due to the difficulty in distinguishing between falling and blowing snow, as snow is the sole source of moisture in these climates.

Annual temperature range

Temperature and fluctuations in temperature have an important influence on soil-forming processes. The map below shows the annual temperature amplitude based on the difference between the mean temperatures of the warmest and coldest months.

This change depends on the annual cycle of incoming solar radiation, which in turn depends on the latitude and altitude, and the proximity of the ocean. Clearly, the Earth exhibits tremendous variations in annual temperature ranges. The map shows nearly mirror patterns of zones either side of the Equator.

The region with the least variation is the equatorial zone. While a significant area displays a modest fluctuation of between 11 and 18 °C this can be as low as 5 - 8 °C. Away from the Equator, the more temperate climate of the savannah regions is clearly evident. What may surprise many people is that the main desert regions display large temperature ranges, with parts of the Sahara registering variations in excess of 40 °C. This is caused by a set of constant high-pressure cells over the tropic of Cancer which give rise to cool winters (approx. 13 °C) and hot summers (> 45 °C).



Map showing the annual temperature range based on the difference between the monthly mean temperature of the warmest and coldest months (derived from Hijmans *et al.*, International Journal of Climatology, 2005). (WCL, JRC) [9]

What controls climate?

- Climate classification systems, like Köppen-Geiger [8], organise the world's climate on the basis of meteorological patterns. These are controlled by:
  - latitude which influences the seasonal range of solar intensity, and evaporation as it is temperature dependent;
  - land heating/cooling faster and more intensely than water; therefore, continental locations have a larger seasonal temperature range than maritime locations. Maritime locations often have more precipitation;
  - geographic position, since issues such as prevailing winds influence local climate;
  - temperature, which generally decreases with altitude. Mountains also affect precipitation patterns;
  - ocean currents, which play a critical role, as sea-surface temperature influences air temperature. Evaporation rates are generally higher where sea-surface temperature is higher;
  - atmospheric pressure patterns and resulting winds, which influence advecting temperature and moisture, cause areas of convergence and divergence and influence mid-latitude storms.

How does climate affect weathering?

- Weathering is the breaking down of rocks and minerals.
- Physical weathering is accentuated in very cold or very dry environments, while chemical reactions are most intense where the climate is wet and hot. Both types can occur together and each tends to accelerate the other.
- Studies have shown that tropical weathering rates, where temperature and moisture are at their maximum, are 3.5 times higher than the rates found in temperate environments.
- When water freezes, its volume expands by 11 %, which can create incredibly high pressures in confined spaces.
- Heating and cooling of rocks causes minerals to expand and contract at different rates. These stresses eventually cause rocks to crack, often by a process known as exfoliation where the outer layers just peel away. Moisture and frost can mitigate these effects.
- Carbon dioxide dissolved in rainwater produces a weak carbonic acid, which can cause weathering of the rocks on which it falls.

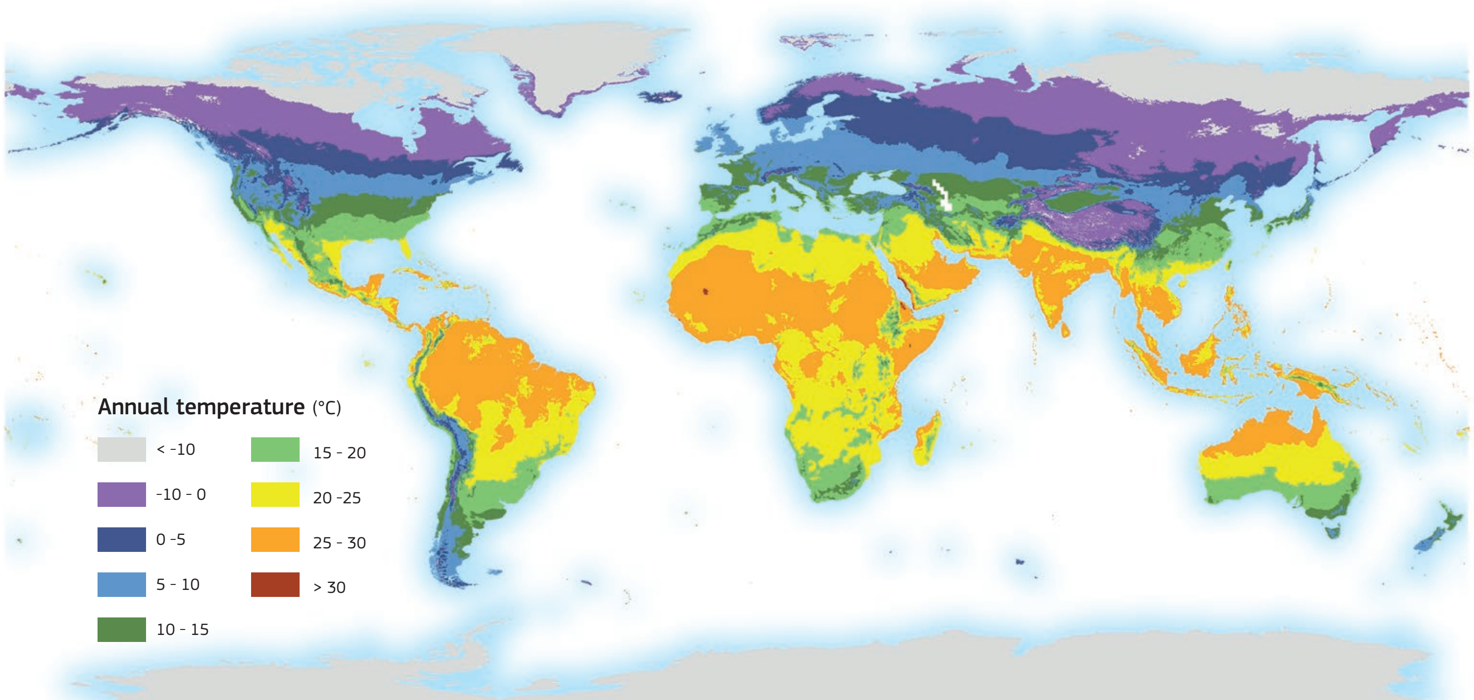
Temperature

The map shows the patterns of mean annual air temperature across the world. The highest temperatures (dark red colour) occur in Mauritania and along the coast of the Red Sea. The highest shade temperature ever recorded in the world was 58 °C at Al Aziziyah, Libya, on September 13, 1922. However, summer temperatures in many parts of the world often reach 46 °C or higher almost every day. In fact, the daily temperatures in the Danakil Depression of Ethiopia and the Eritrean lowlands are consistently higher than 40 °C and can regularly reach 50 °C. During the night, temperatures may drop sharply. Several deserts show large seasonal temperature ranges.

Temperatures measured directly on the ground may significantly exceed air temperatures. A ground temperature of 93.9 °C was recorded in Furnace Creek, Death Valley, California, USA in July 1972, which may be the highest natural surface temperature ever recorded. More recently, satellite measurements of ground temperature taken with the MODIS infrared spectroradiometer on the Aqua satellite recorded a maximum temperature of 70.7 °C in the Lut Desert, Iran. However, these measurements are lower than the maximum point surface temperature as they reflect averages over large areas and include atmospheric attenuation, or gradual loss of intensity. Researchers have calculated that the theoretical maximum possible ground surface temperature should be between 90 and 100 °C for dry, darkish soils of low thermal conductivity.

To many people's surprise, temperatures near the Equator are not excessively high, with average daily temperatures being a constant 24 - 27 °C throughout the year. Extensive cloud cover and heavy rainfall prevent temperatures from rising much higher than 33 °C. The diurnal temperature change (i.e. between day and night) is usually between 2 °C and 5 °C, which is greater than the annual temperature range of 2 °C.

The coolest regions (light grey and purple) are, as expected, in the Arctic and in the high mountain ranges. The lowest temperature ever recorded on Earth was −89.2 °C at Vostok Research Station, Antarctica, although a temperature of −93.2 °C was measured by the Landsat 8 satellite for an unnamed Antarctic plateau on August 10th, 2010.



Map showing the pattern of mean annual temperatures across the Earth. Large parts of the planet are characterised by extreme temperatures (i.e. > 25 °C or < 0 °C) which are not conducive to soil biodiversity (derived from Hijmans *et al.*, International Journal of Climatology, 2005). (WCL, JRC) [9]

Is precipitation only about rain?

- Precipitation is any product of the condensation of atmospheric water vapour that falls under gravity.
- The main forms of precipitation include drizzle, rain, sleet, snow, graupel (soft hail or snow pellets) and hail.
- Precipitation occurs when a portion of the atmosphere becomes saturated with water vapour, so that the water condenses and 'precipitates'.
- Fog, mist and dew are not considered as precipitation. While low compared to rain, their contribution can be significant ecologically, especially in arid climates. Dew is also a habitat for plant pathogens, such as the protist *Phytophthora infestans* (see page 37), which infects potato plants.

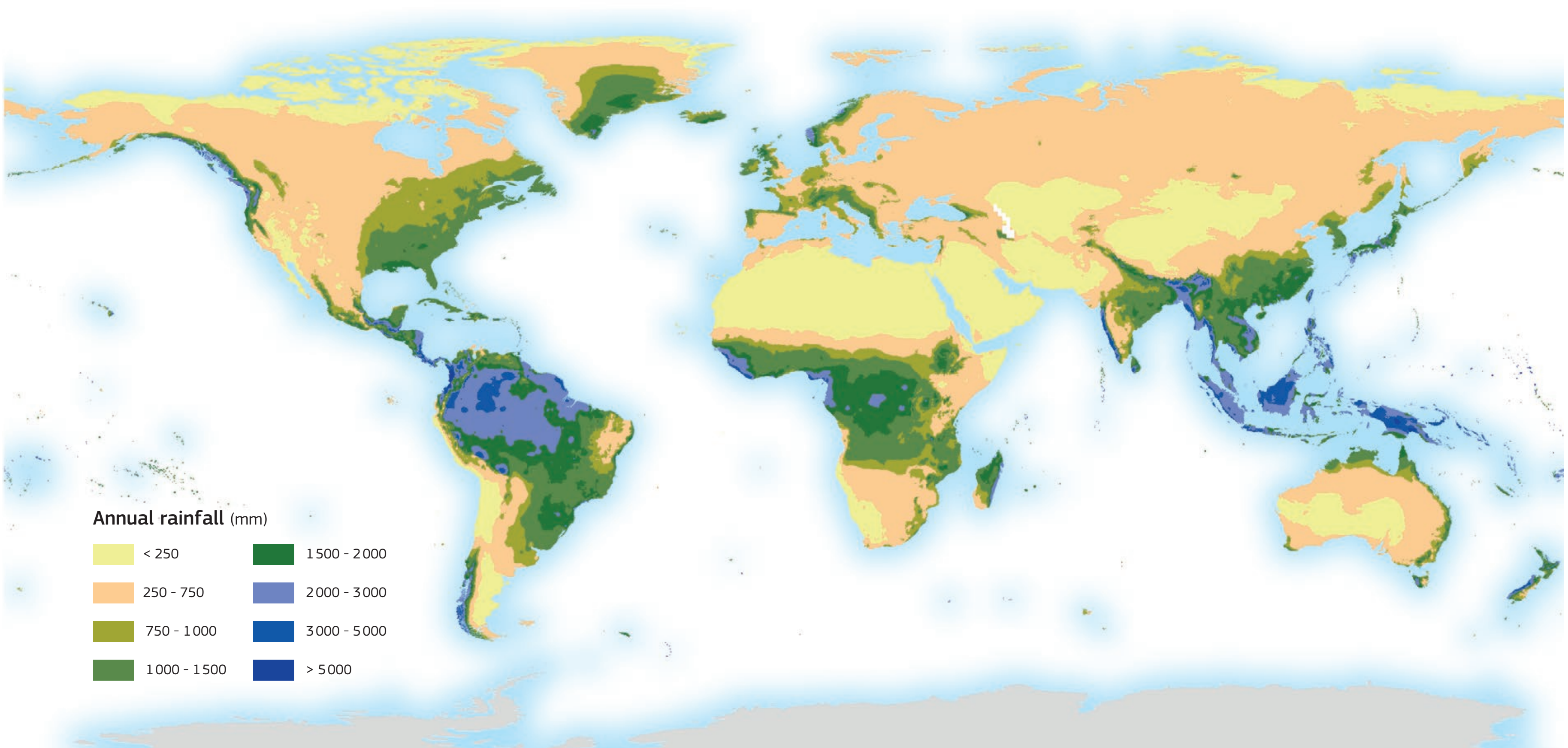
Precipitation

The map below shows the pattern of mean annual precipitation (millimetres of rainfall and the water equivalent of snowfall). Climate classification systems, such as Köppen-Geiger, use average annual rainfall to help differentiate between climate regimes. Precipitation is measured using rain and snow gauges; however, rainfall can also be estimated by weather radars and satellites.

Rainfall is distributed very unevenly across the planet. Many areas receive either too much rain or too little. In parts of the west coast of Africa, for example, annual rainfall averages more than 3 000 mm. In the city of Monrovia, Liberia, more than 1 000 mm of rain falls on average during the month of June alone. By contrast, more than half of Africa receives less than 500 mm of rainfall yearly, while rain may not have fallen for many years in some parts of the Atacama Desert or Arabian Peninsula. The wettest place in the world is Cherrapunji, situated on the southern slopes of the Eastern Himalaya in India, with an average annual rainfall of 11 430 mm. The highest recorded rainfall in a single year was 22 987 mm in 1861. In the tropical rainforest climate, all 12 months have an average precipitation of at least 60 mm. In relation to soil formation, humid conditions lead to more chemical weathering, higher levels of organic matter and leaching of minerals and organic matter. Heavy or prolonged rain can lead to soil erosion and saturated soils. A lack of rain will give rise to the development of crusts and accumulation of salts.

Antarctica is the driest continent. The globally averaged annual precipitation over the whole Earth has been estimated at 990 mm but drops to 715 mm over all land masses.

Prolonged and widespread droughts, such as those found in the Sahel regions of Africa in 1973, can cause much suffering and social unrest. Changes in precipitation patterns can also have a marked effect on soil organisms.



Map showing the pattern of mean annual precipitation. Large parts of the Earth have a mean annual rainfall of less than 750 mm (see correspondence with temperature map above). However, some parts of West and Central Africa, the Far East and the Amazon Basin receive more than 5 m of precipitation every year (derived from Hijmans *et al.*, International Journal of Climatology, 2005). (WCL, JRC) [9]

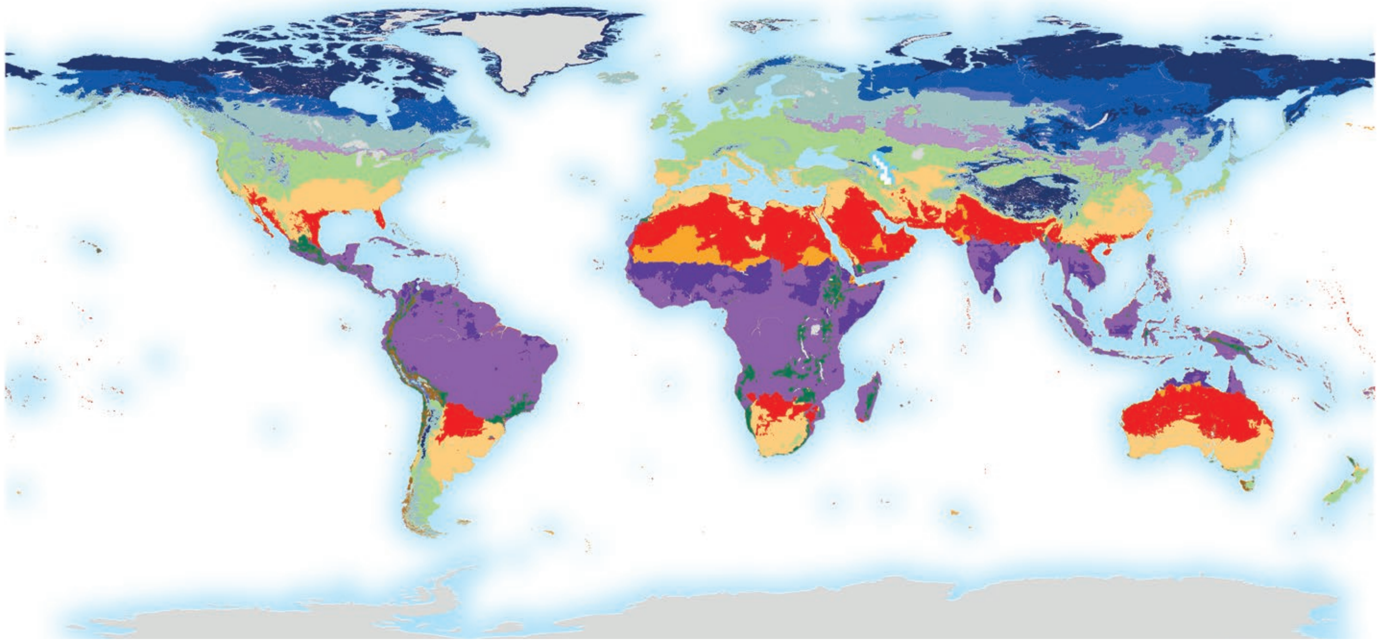
Soil-forming factors – Climate

Soil temperature regimes

Soil temperature is an important attribute and key environmental factor in determining soil-forming processes, the natural distribution of plants and the control of biological processes in the soil. Soil temperatures above or below critical limits severely inhibit seed germination, even if there is adequate soil moisture. The life cycles of many soil-borne pests and diseases are controlled by soil temperature. The temperature of the subsoil lags behind air temperature, commonly by one or two months. The length of lag depends on climate, shade, aspect, the thickness of the organic layer and the thermal conductivity and heat capacity of the soil (governed by factors such as mineralogy and porosity, i.e. how well the soil absorbs water). The map on the right shows the pattern of the main soil temperature regions across the world (for a depth of 50 cm). The classes are:

- Gelic: from the Latin gelare, to freeze. These soils are associated with permafrost and have a mean annual soil temperature (MAST) at or below 0 °C. Gelic soils can be further divided into Pergelic (MAST between −4 °C and −10 °C) and Hypergelic (MAST < 10 °C)
- Cryic: very cold soils but no permafrost. MAST between 0 °C and 8 °C
- Frigid: soils are warmer in summer than in the cryic regime, but their MAST is still between 0 °C and 8 °C and the difference between mean summer and winter soil temperatures ≥ 6 °C
- Mesic: MAST is 8 °C or higher but lower than 15 °C; the difference between mean summer and winter soil temperatures ≥ 6 °C
- Thermic: MAST ≥ 15 °C but lower than 22 °C; the difference between mean summer and winter soil temperatures ≥ 6 °C
- Hyperthermic: MAST ≥ 22 °C and difference between mean summer and winter soil temperatures ≥ 6 °C
- Megathermic: MAST ≥ 28 °C

The prefix 'iso-' indicates that the difference between mean summer and mean winter soil temperatures is lower than 6 °C.



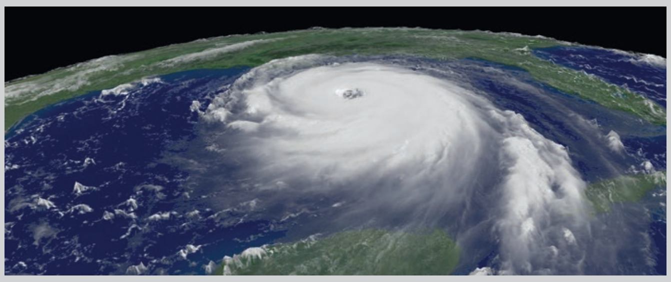
Soil temperature regimes

Hypergelic | Cryic | Thermic | Isomesic | Isomegathermic
Pergelic | Frigic | Hyperthermic | Isothermic | Water bodies
Gelic | Mesic | Megathermic | Isohyperthermic | Rock and ice

Map showing the pattern of soil temperature regimes, an important factor in determining both soil-forming and biological processes operating in the soil. (USDA, JRC) [10]

Extreme weather

- Extreme weather is when a weather event is significantly different from the average or usual weather pattern. This may take place over one day or a longer period of time.
- Flash floods, heat waves and strong winds and storms are examples of extreme weather.
- For example, the hurricane Patricia (October, 2015) sustained wind speeds of more than 340 kilometres per hour.
- The types of extreme weather events (e.g. drought) that would be expected to occur more often in a warming world are increasing.

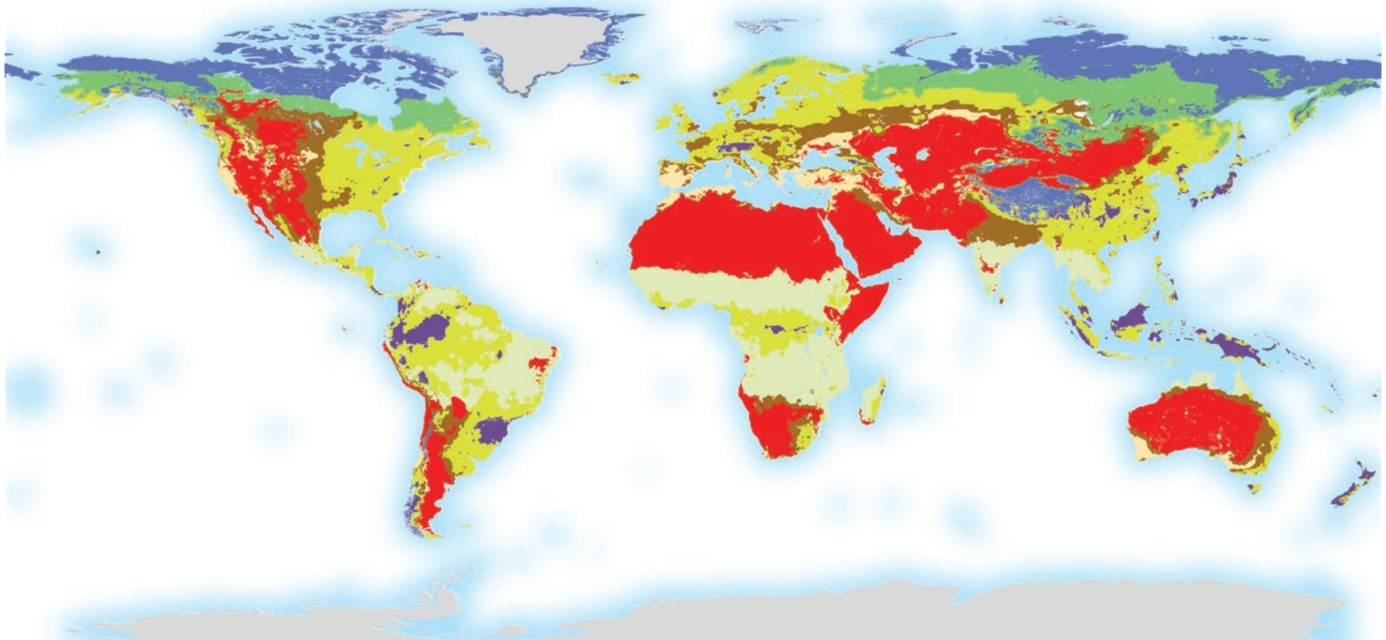


View of a hurricane from space. (NASA)

Soil moisture regimes

Soil moisture regimes are based on the water table level and the presence or absence of water that can be used by plants. Soil moisture regimes affect soil formation and the use or management of soils. Soil moisture regime classes include:

- Permafrost: soil material remains below 0 °C for two or more years in succession. Water occurs predominantly as ice in the form of lenses, veins, crystals and wedges
- Interfrost: cold winters where soil moisture freezes for several months of the year. Can have snowfall
- Udic: humid climate. Soils usually moist all year round; therefore, irrigation is not generally required for crop production
- Ustic: semi-arid climate. Rain falls during the growing season. Generally dry in summer
- Xeric: semi-arid or Mediterranean climate. Soils can be wet in winter but dry in summer. Dryland cropping possible from stored soil water
- Aridic: arid climate, usually dry. Irrigation required for crop production. Dry for significant periods. Soils display little or no leaching and soluble salts tend to accumulate
- Perudic: precipitation exceeds evapotranspiration in all months, but soil is not saturated for long periods
- Aquic: soil is saturated with water long enough to cause anaerobic conditions (not visible on the map)



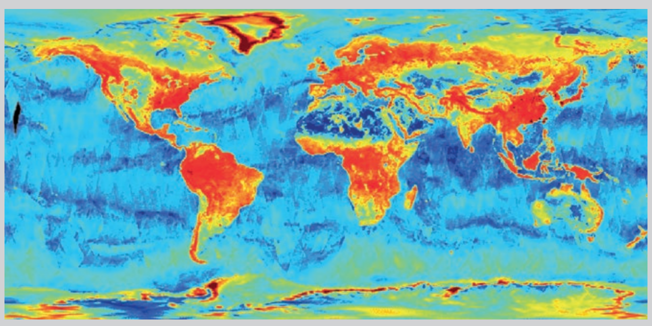
Soil moisture regimes

Permafrost | Aridic | Tropustic | Udic | Water bodies
Interfrost | Xeric | Tempustic | Perudic | Rock and ice

Map showing the pattern of soil moisture regimes. The prefixes 'trop-' and 'temp-' within the Ustic class denote differences in soil temperature. In this context, tropustic indicates warmer conditions. (USDA, JRC) [11]

Soil moisture estimated from satellites

- One of the main controls on the distribution of soil organisms is soil moisture, which could be affected by climate change.
- In recent years, increasingly accurate assessments of actual soil moisture conditions have been provided by sensors on-board satellites.
- NASA's Soil Moisture Active Passive (SMAP) mission (a sophisticated satellite-based radar sensor) mapped global soil moisture levels. Data were gathered from March 31st to April 3rd, 2015.
- In the map below, blue areas denote low soil moisture or lack of vegetation, such as in deserts, while red areas are forested. In-between colours denote subtle differences in soil moisture levels.



Global map of soil moisture. (NASA/JPL/GSFC)

Soil-forming factors – Living organisms

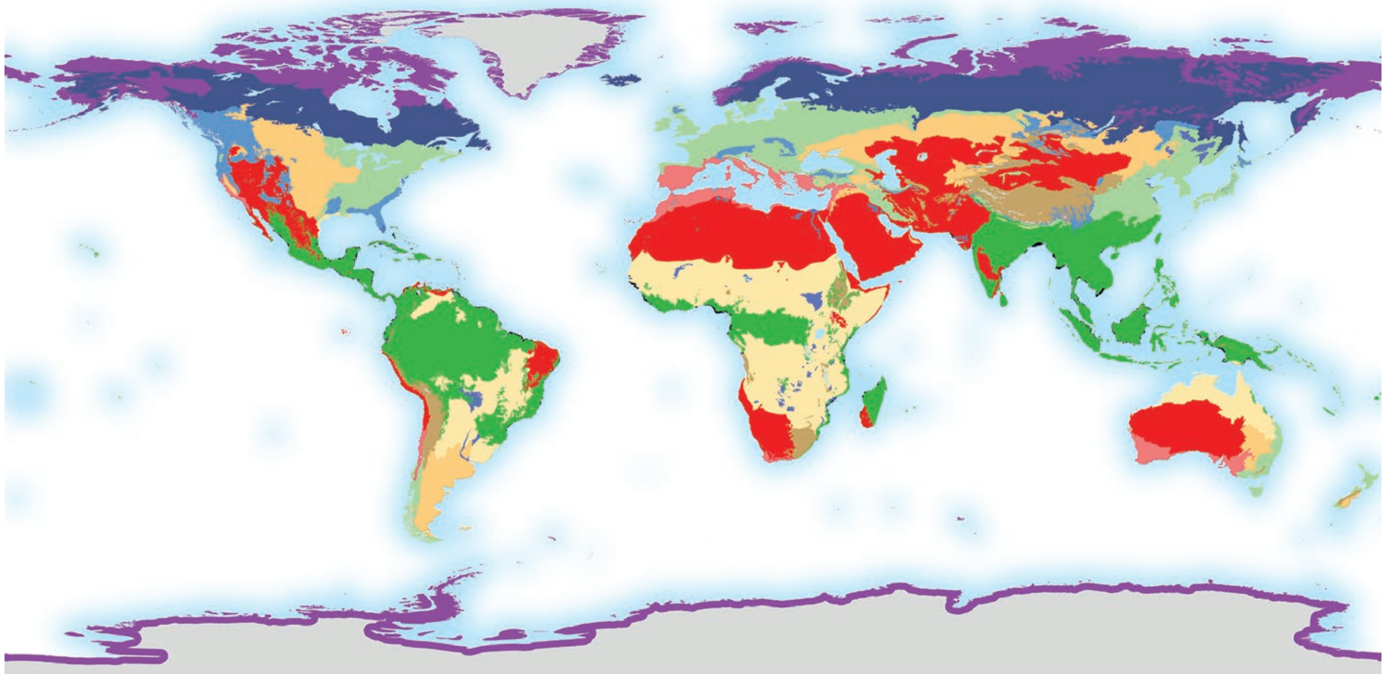
All plants and animals (from microorganisms to humans) affect soil formation. Living organisms add organic matter – a key component of soil – through the breakdown of litter, decomposition of dead roots and the conversion of compounds exuded (i.e. released, from living roots – see page 43). Microorganisms, especially fungi and bacteria (see pages 33-35, 38-41), facilitate chemical exchanges between roots and the soil to produce essential nutrients. Both animals and plants allow moisture and gases to seep into deeper layers along burrows and root channels. Humans can impact soil formation through land management practices that disturb natural processes and change the chemical and physical characteristics of the soil.

Cultivation practices and burrowing animals mix soil from different horizons, especially from the organic-rich surface layers. The nature of biological activity in the soil is governed by climate, topography and soil characteristics, such as depth, texture, structure and chemistry (e.g. pH and salinity).

Ecoregions and biomes

Ecoregions can be defined as relatively large units of land or water containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change. The limits of ecoregions generally follow continental boundaries or major barriers to plant and animal distribution (such as the Himalayas and the Sahara).

Ecoregions are classified by the presence of biomes, which are major plant communities determined by rainfall and climate. Forests, grasslands (including savannah and shrubland) and deserts are distinguished by climate (e.g. tropical, subtropical and temperate) and water conditions. In addition, forests are divided into conifers, broadleaf or mixed.



Ecoregions

- Tropical and subtropical forests
- Temperate broadleaf and mixed forests
- Temperate coniferous forests
- Boreal forests/taiga
- Tropical and subtropical grasslands, savannas and shrublands
- Temperate grasslands, savannas and shrublands
- Flooded grasslands and savannas
- Motane grasslands and shrublands
- Tundra
- Mediterranean forests, woodlands and scrub
- Deserts and xeric shrublands
- Mangroves
- Oceans and inland water
- Rock and ice

Map showing the major ecoregions as defined by the World Wide Fund for Nature (WWF – derived from Olson *et al.*, BioScience, 2001). (WWF, JRC) [12]

Land cover

The term 'land cover' is used to describe the physical material at the surface of the planet. While predominantly vegetation, it can also be bare ground, water or artificial surfaces. Depending on the scale of observation and complexity of the cover type, the eventual classification may be a mixture of the above. It is important to distinguish between the terms 'land cover' and 'land use'. For example, a land cover of mixed shrubs and grass could be used as a park, an orchard or savannah.

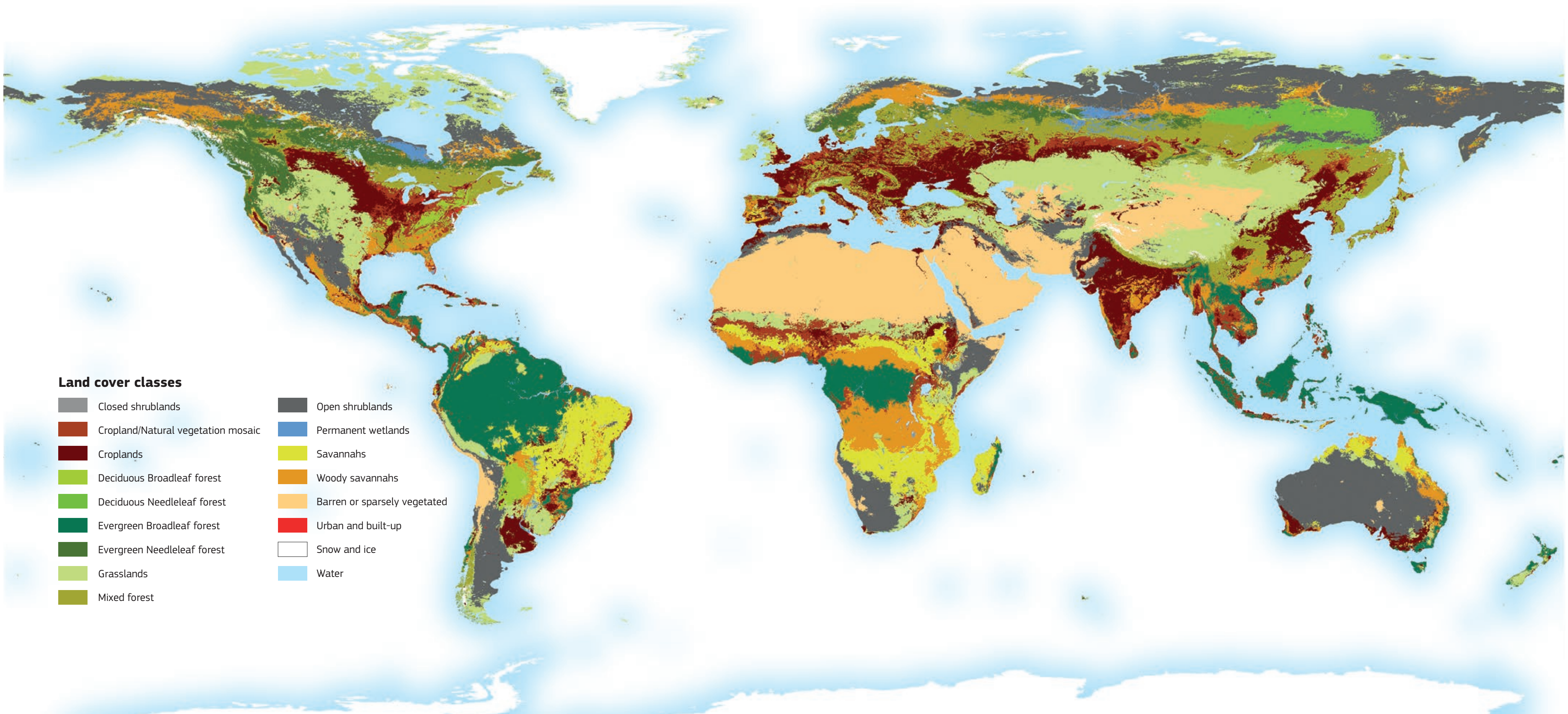
The map below shows the principal types of land cover in 2012 as mapped by satellites orbiting the Earth. The map shows that equatorial regions are covered by extensive forests, which merge to the north and south with open woodland and increasing grasslands or savannah.

Mid-latitudes are characterised by aridity giving rise to bare or sparsely vegetated areas. More temperate climates display a mosaic of croplands and forests that indicates the human alteration of natural vegetation patterns. Northern latitudes show mixed and conifer forests, which give way to the open shrubland of the tundra. At this scale, only the largest urban areas are visible. While trees cover around 27 % of the planet, it is estimated that around three-quarters of the Earth's vegetated surface have been altered by prolonged human activities (see pages 18-19).

Share of global land cover

- Bare soil and rock: 15.2 %
- Croplands: 12.6 %
- Grasslands: 13.0 %
- Herbaceous vegetation: 1.3 %
- Inland water bodies: 2.6 %
- Mangroves: 0.1 %
- Shrub-covered areas: 9.5 %
- Snow and glaciers: 9.7 %
- Sparse vegetation: 7.7 %
- Tree-covered areas: 27.7 %

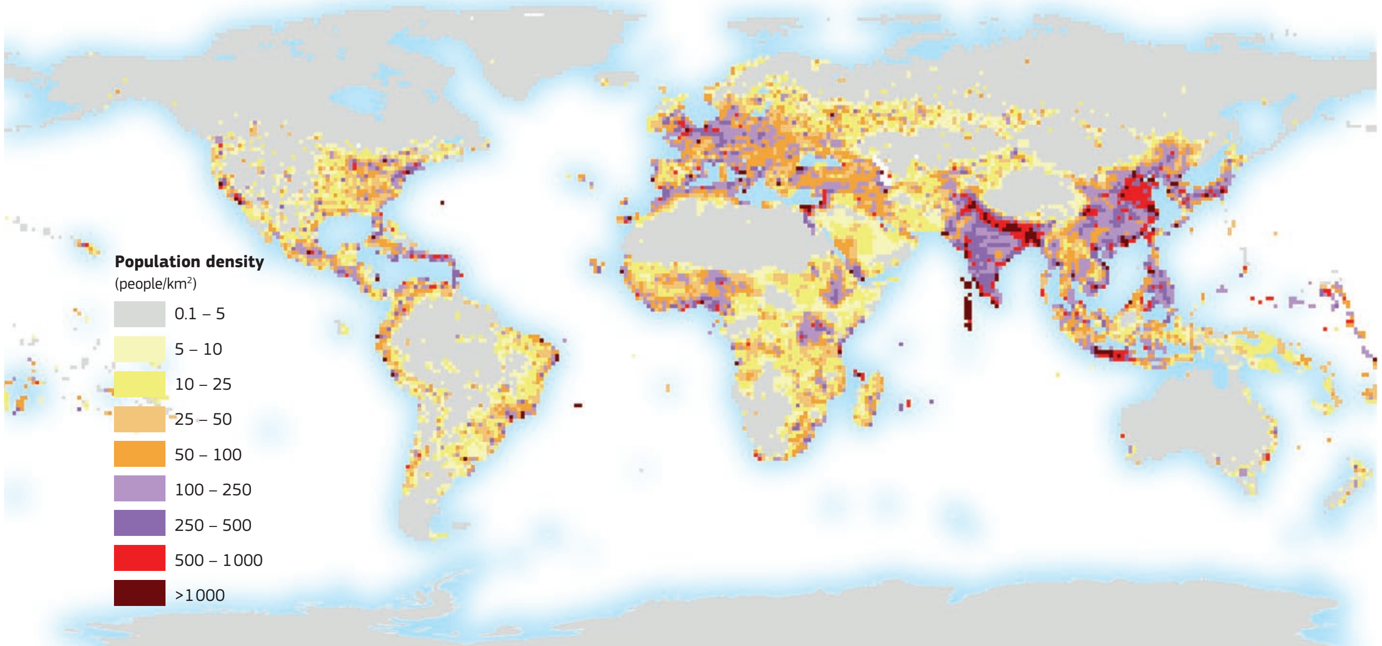
FAO [13]



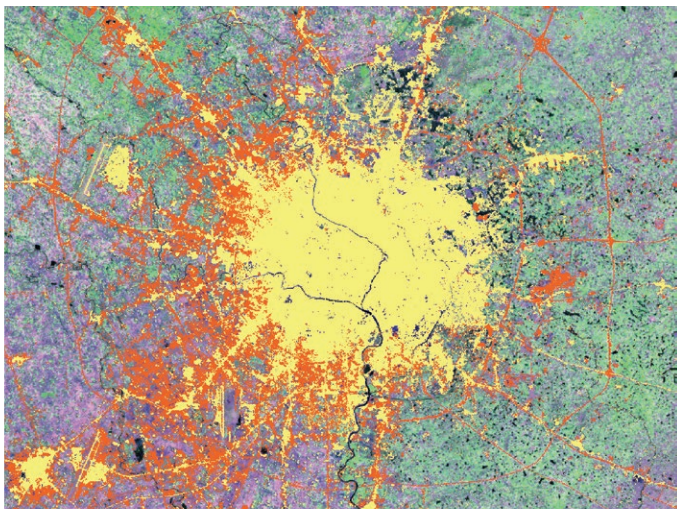
Land cover map for the year 2012 produced using data collected by the MODIS (Moderate-resolution Imaging Spectroradiometer) sensor on board the Terra Satellite. One of the major issues with land cover maps is that most surveys define similar categories in different ways (e.g. forests can vary depending on tree density, tree height, legal standing or ecological function). (NASA) [14]

Soil-forming factors – Human activities

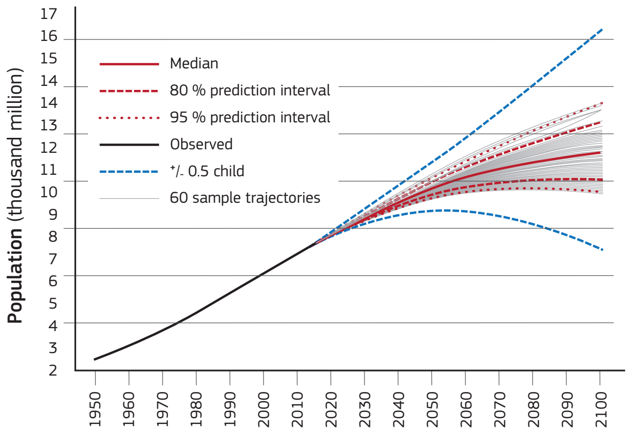
Originally, human settlement was closely dependent on climate, the availability of water, the length of the growing period and the presence of fertile soils for crops and fodder. As a consequence, the urban pattern and infrastructure network that is visible today reflects the areas that match these conditions. The map on the right shows global population density (technically this is the estimated number of people living within one square kilometre). This map denotes where people are concentrated; from the less populated white areas to the densely populated red and purple regions. Population density is generally very low in arid, cold and mountainous regions while the Nile Delta, the Ganges Plain and the Far East are amongst the most densely populated areas on the planet. Average global population density (excluding Antarctica) is estimated at around 50 people/km². However, over half of the land surface is inhospitable. The most densely populated region is the North Indian River Plain with 1 000 people/km².



Map showing the estimated population density of the Earth in 2015. The values denote the number of people living in one square kilometre. While the world's population is currently estimated at just over seven thousand million, it is not evenly distributed across the planet. Over half of the Earth's land mass is inhospitable to humans, which means that people tend to cluster around seaports and fresh water sources. The most densely populated regions in the world are the Taiheiyo Belt (Japan), the southeast coast of China (Guangdong, Hong Kong, Fujian), Java, the North Indian Plain (Pakistani Punjab to Bangladesh and Assam) and the Nile Delta. Urban populations rely almost entirely on third parties for food production, which in turn puts increasing pressure on rural soils. (CIESIN, JRC) [15]



Map of Chengdu (China) shows how the city grew dramatically between July 1990 and July 2000. In this image, yellow areas show the extent of the urban area in 1990, while orange areas show what was built up in the subsequent 10 years. Urban expansion has mostly been on the western side of the city, approaching the mountain foothills, along roadways that radiate out from the city like the spokes of a wheel. A new orbital roadway makes an orange ring around the city. (NASA)



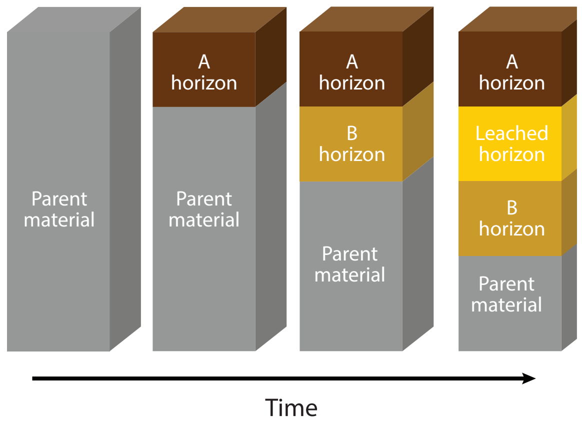
Long-term global population growth is difficult to predict. Projections from the United Nations show a continued increase in population in the near future with a steady decline in population growth rate. The graph shows estimates of the total world population to 2100 based on the projections of total fertility and life expectancy at birth. Global population is expected to reach between 8.3 and 10.9 thousand million by 2050. Increased pressure on land resources in relation to drivers such as urbanisation, climate change and food security will affect soil processes. (UNEP) [16]

Agricultural practices are among the most impacting factors on soil formation and development. (RF)

This night-time satellite image shows the location of lights on Earth's surface. Each white dot represents cities, fires, ships at sea, oil well flares or other light sources. While Western Europe and much of the North African coast is glowing with night lights, the Sahara and much of south-central Africa are largely devoid of illuminated cities. It should be noted that this pattern also reflects the lack of infrastructure in many rural communities where a constant electricity supply is not available or not used for lighting. Two of the most striking features on this image are the high concentration of cities on the River Nile, along the Mediterranean coast of North Africa, the Gulf of Guinea and the urban conglomeration of Pretoria and Johannesburg in South Africa. This view of the Earth at night is a composite of several images acquired by the Suomi National Polar-orbiting Partnership (Suomi NPP) satellite over nine days in April 2012 and 13 days in October 2012. It took 312 orbits and 2.5 terabytes of data to get a clear shot of every parcel of the Earth's land surface and islands. (NASA)

Soil-forming factors – Time

While soils are formed through the combined effect of physical, chemical and biological processes which operate over hundreds or thousands of years, these factors rarely remain constant. Time determines the duration for which a set of factors is active. Over geological timescales, new sources of parent material can be introduced to the landscape while changes in global climate patterns are usually accompanied by changes in sea-level, erosion and deposition regimes, vegetation patterns and the shape of the landscape. Over much shorter timescales (100–1 000 years), major changes can occur in the amount and nature of biological activity or hydrological conditions within a soil. Even annual fluctuations in weather patterns (e.g. drought or above-average rainfall) or changes in the use of the land (conversion of forest to arable farming) can affect soils. Dramatic changes in soil-forming factors can either lead to an increase in the rate of soil formation or to the destruction, or even complete removal, of the soil. Given constant environmental conditions, all soils must eventually tend toward a state of equilibrium or maturity where the rate of soil formation is equal to the rate of soil loss. However, situations may arise naturally where the rate of destructive processes exceed the rate of accumulation and retention of materials from weathering, plant growth and aerial deposition. At this point, the soil and its biodiversity become vulnerable to degradation processes, such as wind and water erosion.



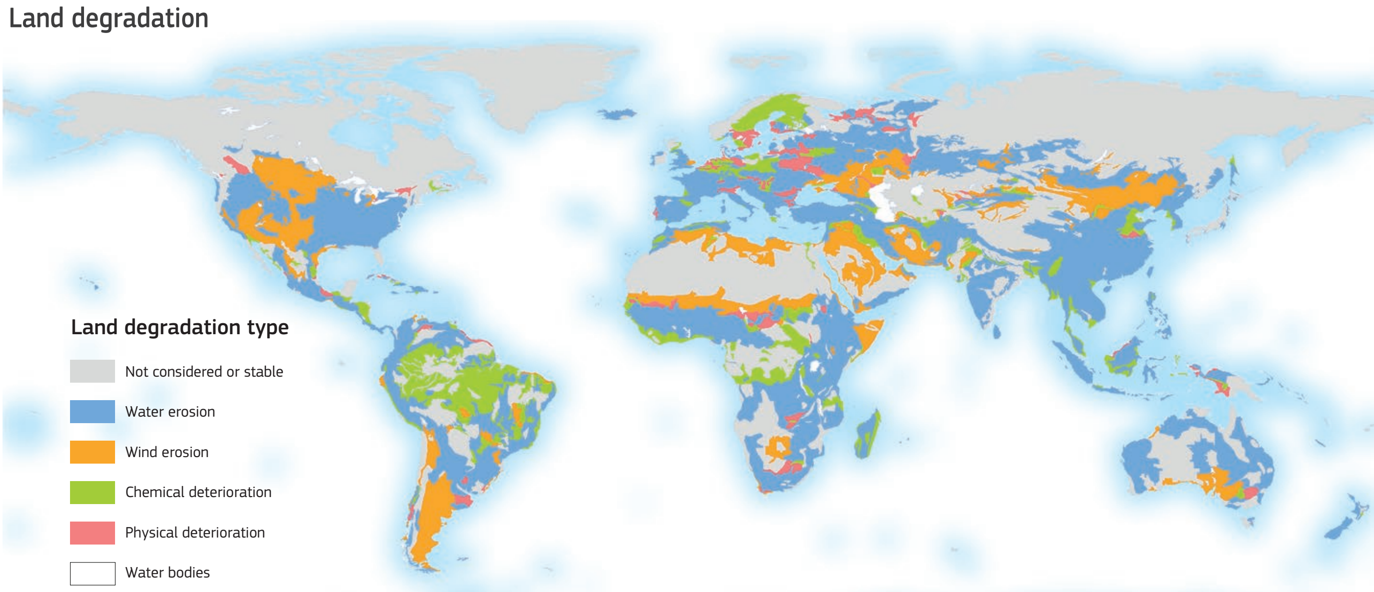
The figure above shows theoretical soil development in a humid environment. Parent material is subjected to weathering while the accumulation and decomposition of organic matter on the surface eventually leads to the development of an A horizon. Much later, soil processes will lead to the development of a B Horizon with accumulations of organic material, clay, iron or aluminium – often derived from the A horizon. In humid climates the upper part of the soil may become leached and an eluvial horizon (or E horizon) is formed. (JRC)

The photograph on the right shows the beginning of soil formation. Horizon differentiation below the surface horizon (i.e. deeper than 25 cm) is weak. The only evidence of soil-forming processes are some brownish discolourations and the formation of structure. Evidence of clay movement or destruction is lacking, as are appreciable levels of organic matter, aluminium and/or iron compounds. This soil contains a large amount of stones and lightly weathered parent material. 'Young', weakly developed soils cover an estimated 15 million km^2 worldwide. They are well represented in temperate and boreal regions that were under the influence of recent glaciation, partly because the soil's parent material is still young, but also because soil processes are comparatively slow. Such soils are less common in the tropics and subtropics. (EM)

How old are soils?

- It is very difficult to accurately assess the age of soils. Since soil-forming factors continue to affect soils during their existence, evidence of earlier cycles may have been destroyed.
- Studies have shown that the rate of soil formation varies from around 100 years for 2–5 cm on volcanic ash in warm humid climates to 1 cm in 5 000 years on hard rocks in cool temperate climates.
- Soils in glaciated areas only formed after the ice melted. In North America and Europe, this makes them thousands of years old.
- Human artefacts and buried organic matter can be dated based on the natural radioactivity present in all organic carbon matter.
- There is much debate about the age of soils in the tropical regions of Africa and South America. Many believe that they are millions of years old. Countering this is the view that soil-forming factors only operate at the surface of deeply weathered sediments.

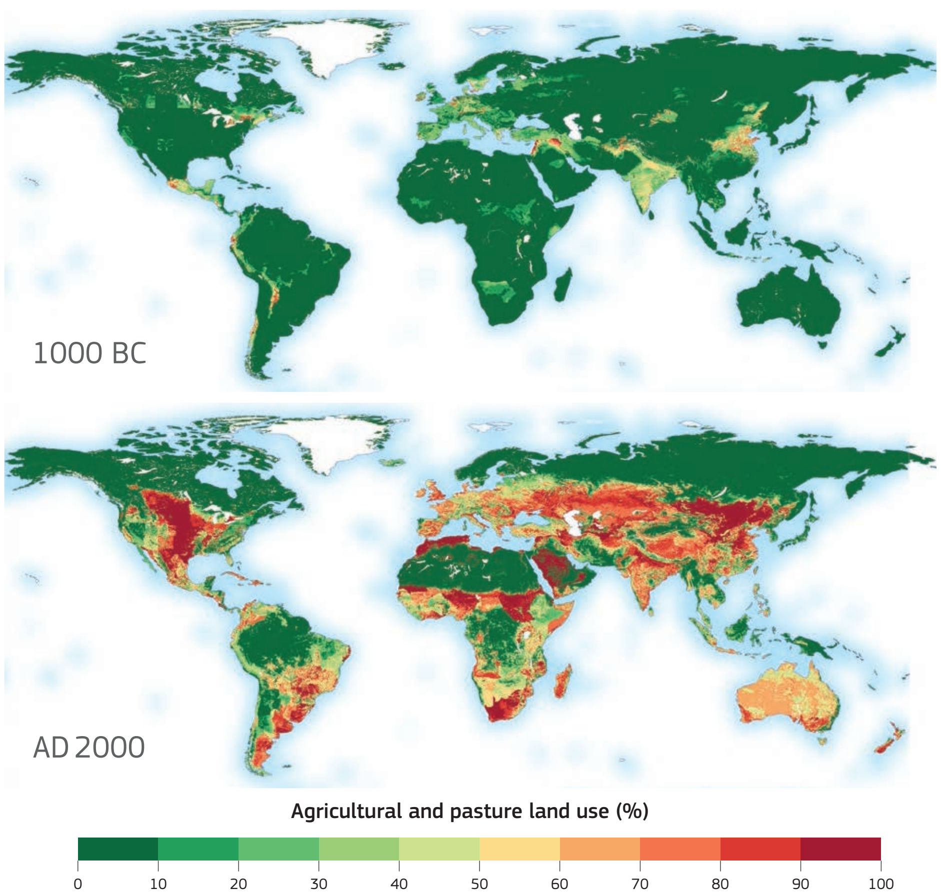
Land degradation



Maintaining soil condition is essential for maintaining several ecosystem services (see Chapter IV) and biological diversity. However, soil is under increasing threat from a wide range of human activities. The threats are complex and, although unevenly distributed, their dimension is continental and they are frequently inter-linked. When many threats occur simultaneously, their combined effects tend to increase the problem. Ultimately, if not countered, soil will lose its capacity to carry out its functions. This process is known as soil degradation. The above map, showing the extent of the four main types of degradation, was produced from data collected by a UNEP-funded project in the mid-1990s to categorise human-induced soil degradation (GLASOD – Global Assessment of Human-induced Soil Degradation). Within the project, the type, extent, degree, rate and main causes of soil degradation were assessed and mapped within loosely defined physiographic areas, according to expert judgement.

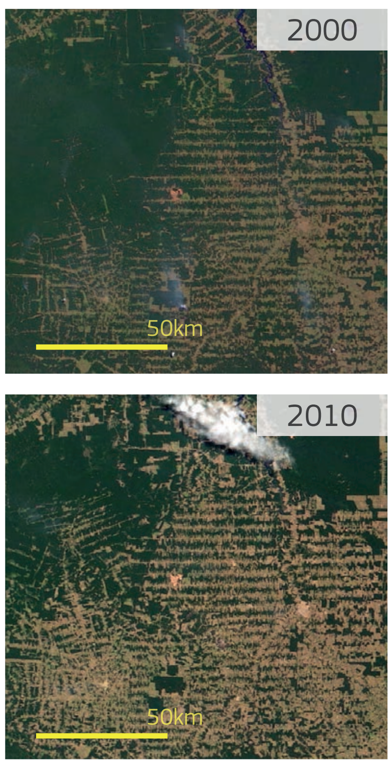
Analysis of the data indicated that around 15 % of the global land surface was degraded or in the process of degrading. Loss of topsoil by water or by wind erosion is by far the most important subtype of displacement of soil material, with water erosion occupying around 56 % of the total area affected by human-induced soil degradation. The area affected by wind erosion occupies a further 38 % of the degraded terrain, while chemical and physical soil deterioration cover about 12 % and 4 %, respectively. While the GLASOD database has been criticised because the qualitative judgements were never tested for their consistency, the database still remains the only global assessment of land degradation. Alternative models are still under development. [18]

Land cover change over time



Humans have transformed most of the terrestrial biosphere into anthropogenic biomes (known as anthromes), resulting in novel ecological patterns and processes. This change has had a profound impact on soils and on the organisms living within them. The above maps, from the KK10 dataset of anthropogenic land cover change over the past 8 000 years, show the extent of change in natural vegetation over the past three millennia (see page 17 for comparison with current land cover conditions). These data show that trends differ dramatically between biomes, with temperate woodlands showing the most intensive and sustained development. Savannahs, shrublands and temperate grasslands show dramatic recent increases in changes while cold boreal woodlands and tundra show little change. While some studies suggest that 50 % of the terrestrial biosphere was transformed by human activities around the 18th century, interestingly, the KK10 model shows that this may have already happened almost 2 000 years earlier. Current conservative estimates indicate that 75 % of all terrestrial habitats have now been affected by human activity, 30 % of which have been transformed into anthromes. A further third are now managed rangelands and semi-natural habitats. Current rates of change in some parts of the world are greater than ever, resulting in unprecedented losses of biodiversity and related ecosystem processes (derived from Kaplan *et al.*, The Holocene, 2010). (JK) [17]

Deforestation



Deforestation is the permanent destruction of natural woodlands through the felling of trees in order to make the land available for other uses (apart from forest). All major tropical forests – especially those in the Americas, Africa and Southeast Asia – are under pressure, largely to make way for human food production, including livestock and crops. Additional drivers are logging and the construction of roads or buildings. The loss of trees destroys habitats and biodiversity, and reduces carbon sequestration and soil functions. Deforestation generally increases rates of soil erosion, by increasing the amount of runoff and reducing the protection of the soil from tree canopy and litter. In some situations, it can lead to the onset of desertification. Therefore, tropical deforestation has profound consequences on soil condition and associated biodiversity.

The state of Rondônia in western Brazil is one of the most deforested parts of the Amazon. This pair of satellite images from the MODIS sensor on NASA's Terra satellite shows the same area in the years 2000 and 2012. On both images, intact forest is deep green, while cleared areas and bare ground are tan (bare ground) or light green (crops, pasture, or occasionally, second-growth forest). Over 12 years, roads and clearings have pushed west from the town of Buritis toward the Rio Jaciparaná River. In this interval, the deforested area along the road to Nova Mamoré has expanded northwards all the way to the BR-346 highway.

Such time series images show that deforestation follows a fairly predictable pattern. The first clearings that appear in the forest show a typical fishbone pattern along the edges of roads. Over time, the fishbones collapse into a mixture of forest remnants, cleared areas and settlements. This reflects the establishment of legal and illegal roads into a remote part of the forest, followed by small farmers who claim land along the road and clear some of it for crops. Within a few years, heavy rains and erosion deplete the soil, causing crop yields to fail. Farmers then convert the degraded arable land to pasture and clear more forest for crops. Eventually, these small farmers either sell or abandon their land to large cattle holders, who consolidate the plots into large areas of pasture. (NASA) [19]

Soil-forming processes

Principle processes

The specific properties of an individual soil type are determined by pedological processes that operate during its lifetime. These biological, chemical and physical actions add, transform, move (translocate) and destroy or remove material within the soil. It is important to recognise that soil-forming processes can evolve and change over time in response to factors such as climatic variability and land use. Many soils exhibit several distinct and different phases of soil formation. More detailed information on the processes described in the following pages can be found in [20, 21].

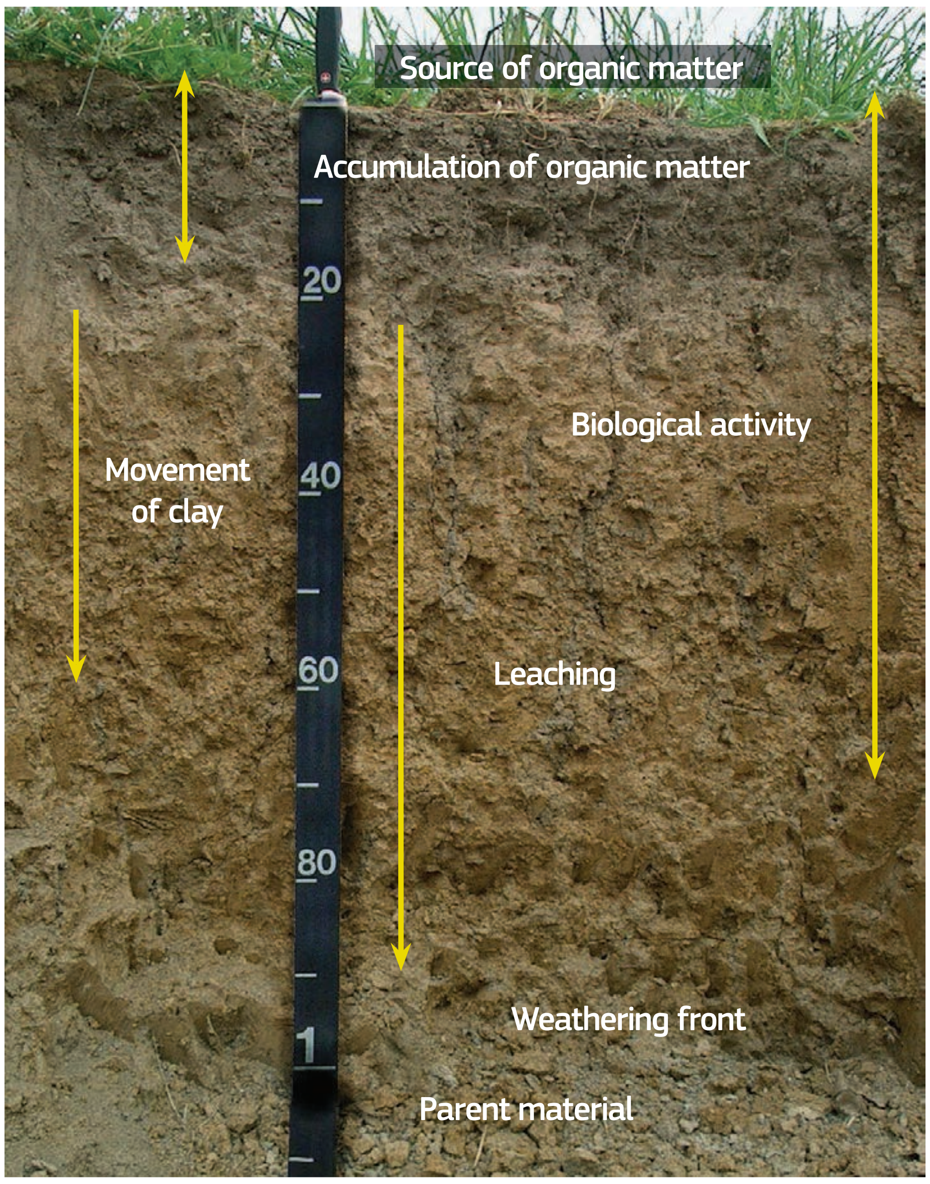
Weathering

Below the soil, solid rock or unconsolidated sediments can be found in (or on) which the soil has developed (see page 12). In reality, all sediments are derived from solid rock by a process known as weathering. Weathering proceeds through a physical destruction of the rock structure which, in turn, facilitates chemical changes to the constituent minerals. In principle, there are two main types of weathering: physical and chemical. Biological activity is also important as it contributes to both types (see below).

Physical weathering

In physical weathering, rocks disintegrate without changing their chemical composition. Typical examples of these processes are the splitting of rocks through daily warming of the sun and cooling during the night (typical of desert environments), or by the repeated freezing and thawing of water (when water freezes, its volume increases by 10 %, causing tremendous pressures if it occurs in confined spaces, such as crevices in rocks).

Physical weathering produces a layer of loose material, which covers the underlying solid rock. This material is known as regolith and can vary from a few millimetres to tens of metres thick. Regolith layers in some parts of west Africa have been found to be more than 150 m thick. There is often a sharp boundary between the bottom of the regolith and the bedrock. This narrow zone is known as the weathering front and is the focus of active weathering.



A schematic of key soil-forming processes. The dark colour of the upper part of this soil profile indicates that significant amounts of organic matter have accumulated in the topsoil through the decay of vegetation and root material. The lighter colour between 20 and 40 cm is caused by a combination of the leaching of mobile iron and loss of clays by percolating rainwater. In the subsoil, the iron has coated soil particles with a thin, reddish film. The parent material from which the soil has developed and the weathering front is clearly visible at the base of the profile. Biological processes are generally more active in the topsoil. (EM, JRC, LJ)

The destruction of bedrock through both physical and chemical weathering is clearly visible in this photograph from South Africa. The red rock is a dolerite dyke that has intruded into granite (visible to the left). It is very evident that the dolerite is weathering more rapidly than the granite. Weathering processes have caused blocks of granite to break away while the dolerite breaks down more easily to produce the distinctive red coloured finer material that is accumulating at the foot of the slope. The dolerite is receding into the cliff face and approximately 15 cm of soil has developed above it, while bare rock is still visible on the surface of the granite. (EM)

Minerals vs. nutrients

- A mineral is a naturally occurring solid substance formed through geochemical processes with a characteristic chemical composition. Rocks are composed of several minerals.
- Nutrients are chemical elements required by organisms to live and grow. Nutrients can be produced by the organism or taken up from its environment.
- Plants absorb nutrients from dissolved minerals in the soil which, in turn, are consumed by herbivores and then by the people who eat the herbivores. People can also obtain nutrients directly from fruits and vegetables. In this way, minerals move up the food chain.

Chemical weathering

Chemical weathering is a gradual and continuous process. It is driven primarily by the reaction between water or an acid and elements within the parent material, which lead to the creation of secondary minerals from the original compounds present in the rock. Chemical weathering is much stronger if temperature and humidity are high (e.g. in the humid tropics).

Water is the key factor in chemical weathering. Most people are unaware that rainfall is slightly acidic with a pH of around 5.6 in unpolluted environments. Atmospheric carbon dioxide dissolves in rainwater to produce a weak carbonic acid. Some minerals, due to their natural solubility (e.g. evaporites such as highly soluble salts and gypsum) or inherent instability relative to surface conditions (e.g. silicate minerals such as feldspar, mica, augite, hornblende and olivine), slowly dissolve to form secondary products, such as clay minerals (e.g. kaolinite, illite, vermiculite and smectite), iron and aluminium (hydr)oxides, carbonates and essential plant nutrients, such as calcium and potassium.

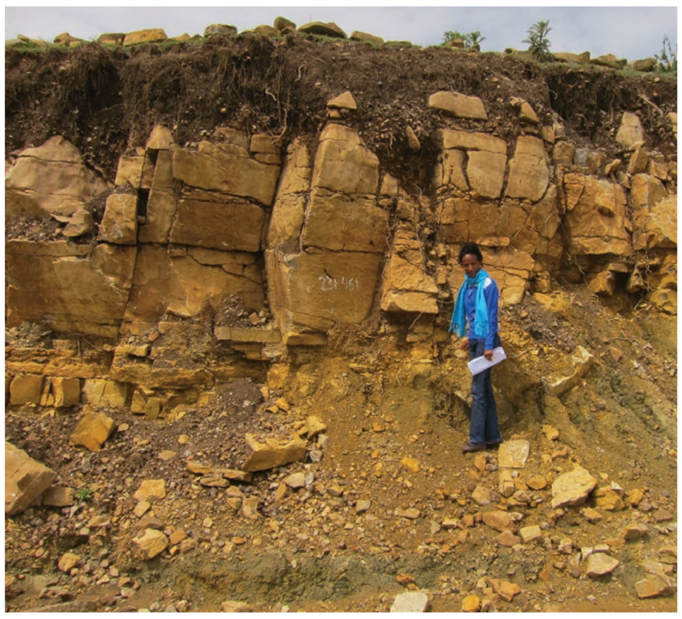
One of the most well-known solution-based weathering processes is de-calcification, which occurs on parent materials that are rich in calcium carbonate, such as limestone and chalk. The weak carbonic acid in rainfall reacts with the calcium carbonate in the limestone to form calcium bicarbonate, which is then removed. This process can be even stronger if gases, such as sulphur dioxide and nitrogen oxides, are present in the atmosphere. These oxides react in the rainwater to produce stronger acids with a pH as low as 3.

Water molecules can break up into positively charged hydronium (H_3O^+) and negatively charged hydroxyl (OH^-) particles (see Glossary for ion and cation). These small and mobile particles can actually penetrate the crystal lattice of silicate and carbonate minerals. Those with positive charge disrupt the balanced state of the mineral in question causing various cations to be released into the soil.

This process is known as hydrolysis and is one of the underlying factors of soil fertility.

Another chemical process involves the simultaneous loss (referred to as oxidation) and gain (referred to as reduction) of electrons in substances. These exchanges are referred to as redox reactions. As materials become oxidised, the unbalanced charge degrades a material's structural composition.

Biological weathering is caused by the activities of living organisms and has both physical and chemical aspects. Examples of physical biological weathering include the loosening of rock by roots growing into cracks and burrowing creatures, such as termites that mix, or churn, the soil. Chemical biological weathering can be caused by bacterial activity or by strong organic acids from plant roots or litter. A recent study demonstrated a three - four-fold increase in weathering rate under lichen-covered surfaces compared to recently exposed bare rock surfaces. Biological weathering factors in Africa are highly significant.



A clear example of a weathering front on limestone in Tigray, Ethiopia. The photograph shows the breakdown of the underlying bedrock along vertical joints and horizontal bedding planes. (JD)

Common processes in humid conditions

Many parts of the world are characterised by a climate that provides a precipitation surplus during some parts of the year (i.e. when rainfall is greater than evaporation rates). This surplus fills the spaces or voids in the soil, which might have been emptied during the dry season, and then percolates down through the soil body to accumulate as groundwater. In doing so, the water drives three important soil forming processes:

Leaching

When water passes through the soil, it dissolves soluble salts (such as chlorides, nitrates, sulphates and carbonates) and flushes them, together with organic and chemical solutes, into the deeper parts of the soil. In drier climates, these salts can be re-precipitated, for example, as a calcium carbonate-rich or gypsum horizon in the subsoil. In more humid regions, significant amounts of materials can be completely removed from the soil.

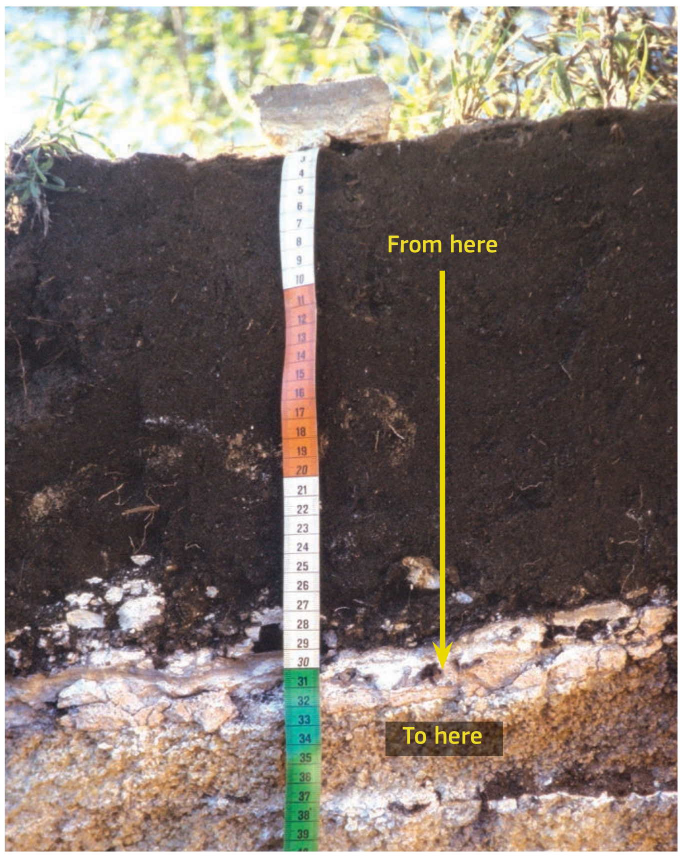
This loss of mineral and organic solutes caused by percolation is known as leaching. The rate and extent of leaching depends on the two following factors:

- the mobility of an element, which is based on its solubility in water and the effect of pH on that solubility – chlorides and sulphates are very mobile, while titanium is insoluble even at a pH of 2.5
- the rate of water percolation, which depends on climate, soil texture and structure, porosity and the slope of the ground – in dry regions, even the most mobile compounds (e.g. sodium chloride) tend to stay in the topsoil and eventually give rise to saline soils

As humidity levels increase, losses of salts, organic compounds and silica in the topsoil increase and the soil is regarded as being leached.

Leaching is a major controller of soil fertility. As long as calcium carbonate is present, the pH of the soil remains above 7 and the soil is often whitish or light-coloured. When the calcium carbonate is dissolved and leached away, the pH drops and calcium, magnesium and sodium are released from the surfaces of clay minerals and humus, to be replaced by hydrogen and aluminium. Unless there is a change in the soil-forming factors or there is human intervention, the soil pH falls below 7 and, under such conditions, the soil is referred to as acidic.

Highly acidic soils are not very suitable for the cultivation of most plants. Such soils require the addition of calcium carbonate (a practice known as liming) in order to raise the pH to a more acceptable level, depending on the crop. A reduction of pH below 5.5 can cause a release of aluminium cations in the soil solution, which is toxic for some plants and nearby water bodies.



A leached soil profile. In this soil, carbonates have been leached from the uppermost 30 cm of the topsoil, which is represented by the dark, humus-rich surface horizon. The white layer below 30 cm shows the accumulation of the leached carbonates deeper in the soil. (OS, JRC, LJ)

In some instances, immobile elements can be leached when they are combined with organic compounds (e.g. organic and amino acids) derived from the humification of litter or from soil microorganisms. This process, known as cheluviation, is an important mechanism for increasing nutrient availability to plants. Chelates are very important in micronutrient management.

The movement of clay particles

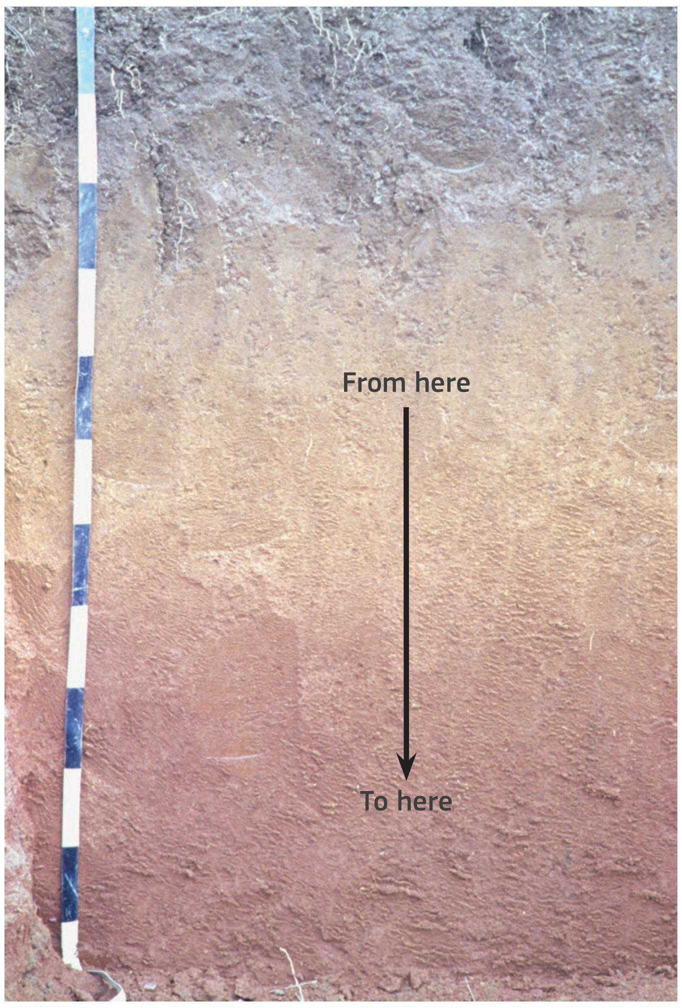
A common soil-forming process is the movement, or translocation, of clay particles from one soil horizon to another. This involves the mechanical transfer of clay particles from the upper part of the soil by percolating water (eluviation) and their re-deposition deeper in the soil (illuviation) on the surfaces of soil particles or in soil pores and cavities.

Clay movement is dependent on the soil texture, structure and chemistry. If a continuous and coarse pore system exists in the soil, percolating water can then transport the clay particles downwards. Such conditions will develop as the soil shrinks and cracks during dry seasons. The clay accumulates where the cracks end and water movement almost ceases, or where the water penetrates into the dry aggregates and the clay particles are filtered at the ped surfaces forming clay layers or skins called cutans or argillans.

Another process that can lead to low clay content in the topsoil is raindrop erosion, where splashes move the finer particles down the slope leaving behind silt and sand. This process is believed to be widespread and appears to be enhanced by shifting cultivation practices on sloping terrain.

Clay destruction

A significant soil-forming process is the destruction of clay. The leaching of base cations leads to the build up of hydrogen ions on clay minerals and organic matter. This state is unstable and leads to the eventual disintegration of the crystalline structure of the clay, releasing aluminium and silica in the process. As a result, the soil exhibits less clay and a lower pH in the topsoil and subsoil immediately below the topsoil than in the main part of the subsoil. Similar clay distribution can be found in soils in which the clay in the topsoil has been redistributed rather than destroyed (see below). Such soils are known to have an argic horizon and typify soils such as Luvisols.



This profile from South Africa illustrates the movement of clay particles from the topsoil to the subsoil. The photograph clearly shows an upper grey layer (0-25 cm) which is a ploughed horizon where the soil has been mixed by cultivation. Directly underneath is a light-toned layer (between 25-70 cm) resulting from the destruction and removal of brown- and red-coloured clay particles. The darker coloured subsoil (> 70 cm) reflects the accumulation of clay particles from above. This process is known as illuviation. (ISRIC, JRC, LJ)

The many sides of clay

- In English, the word 'clay' can have three distinct meanings:
  - a small soil particle, less than 2 µm in diameter;
  - a textural class containing more than 40 % clay particles, less than 45 % sand and less than 40 % silt;
  - a naturally occurring material composed primarily of fine-grained minerals, which is generally a plastic substance at appropriate water contents that will harden when dried or fired. Although clay usually contains phyllosilicates, it may contain other materials that impart plasticity and harden when dried or fired.

This profile illustrates the initial stages of soil formation. The only apparent pedogenic processes are the development of soil structures and changes in colour. This example shows a thin accumulation of organic matter on the surface and the leaching of iron (lighter patches). Such soils are widespread in recently deposited parent material or in regions that have been tectonically uplifted. (JD)

Podzols – very leached soils

- A Podzol is a soil type characterised by the presence of a dark subsurface deposition layer (known as a spodic horizon), overlain by an ash-grey, strongly leached eluvial horizon.
- Podzols can occur given a specific combination of high precipitation, a coarse-grained and silica-rich parent material (e.g. river sands) and vegetation that releases strong organic acid from its litter as it decomposes. This process is called podzolisation.
- These acids mobilise metal oxides in the topsoil. Percolating water redeposits them deeper into the soil, leaving behind a zone of bleached, immobile sand grains.
- The redeposited mix of iron and aluminium can form a hardened or cemented horizon which acts as a barrier to the passage of further leached material and roots. Precipitating iron can give a uniform orange-red colouration to this horizon.
- Over time, organic matter accumulates on this obstruction where a dark, humus-rich sub-surface horizon develops.
- Podzols are found on all continents but predominantly in the temperate and boreal regions of the Northern Hemisphere.

This striking example from Belgium clearly shows the light-coloured bleached horizon overlaying both a darker and a reddish horizon where leached organic matter and iron (respectively) have accumulated. (SD)

Soil-forming processes

Common processes in a wet tropical climate

A significant part of the world has a humid tropical climate, where constant high temperatures (average annual temperature is around 26 °C), copious rainfall (over 2 000 mm annually) and high humidity occur throughout the year. In addition, much of tropical Africa and South America is characterised by old, geologically stable landscapes that have been deeply weathered. Under such conditions, chemical weathering, leaching and translocation combine to produce a number of distinctive soils where the geology of the bedrock determines the underlying chemical properties of the soil. The most typical divisions are:

Highly weathered soils with a ferralic horizon

In deeply weathered sediments, a combination of high soil temperature and intense percolation dissolve and remove all weatherable primary minerals from the soil. Less soluble compounds, such as iron and aluminium oxides, the clay mineral kaolinite and coarse quartz grains, remain behind. This process eventually leads to the formation of a ferralic horizon. High concentrations of hematite (an iron oxide) give a distinctive red colouration to the soil, while in more temperate conditions, the mineral goethite tends to dominate, giving soils a more yellow colour. To be effective, the process requires low soil pH, geologically stable land surfaces and basic parent material containing abundant levels of iron and aluminium in the form of easily weatherable minerals but little silica. Clay content and texture are relatively constant with depth due to the mixing of the soil by biological activity (primarily termites). Soils matching these characteristics are referred to as Ferralsols. Such soils can support luxuriant natural vegetation (e.g. rain forest), due to a self-sustaining nutrient cycle. If this cycle is broken (e.g. as a result of deforestation), the soil quickly loses its fertility and is prone to degradation processes, such as erosion. Traditional agricultural practices of temporary forest clearance and shifting cultivation recognise this cycle.

Weathered soils with a distinctive nitric horizon

A derivation of the ferralisation process described above can lead to the development of soils containing a characteristic 'nutty', polyhedric (i.e. many-sided), blocky structure with shiny ped faces. Typically, the soil body is deep, developed in fine textured weathering products of intermediate to basic parent material and contains high levels of kaolinite and iron (hence the red colour). In some respects, these soils could be seen as young examples of the ferralisation process. Following the intensive weathering and leaching of minerals, alternating micro-swelling and shrinking episodes produce well-defined structural elements with strong, shiny pressure faces. Through biological activity (pedoturbation), the soil can become highly mixed, resulting in a characteristic crumbly or subangular blocky soil structure and diffuse soil horizon boundaries. The spatial distribution of this process is highly dependent on subtle variations in the landscape and parent material. Soils matching these characteristics are known as Nitisols.

Soils with an iron-rich horizon that can harden (plinthic)

On level or gently sloping terrain, a substance known as plinthite (from the Greek *plinthos*, meaning brick) can develop in iron-rich parent material that is prone to fluctuating groundwater levels. Plinthite is a subsurface accumulation of iron (hydr)oxides, kaolinitic clay and quartz. Plinthite is generally formed through the segregation of iron in the soil that has been saturated with water throughout the year. The iron has probably been transported by soil water from higher ground as ferrous iron under anaerobic conditions. Alternatively, iron concentrations may increase due to the removal of silica and base cations through the leaching of dissolved weathering products. The resulting ferrous iron is precipitated as soft, clayey, red or dark-red ferric iron concretions. Soils with these characteristics are referred to as Plinthosols. If enough iron has precipitated and the soil starts to dry out, the soft clay begins to harden irreversibly on exposure to the open air.

Hardened plinthite occurs in concretionary (skeletic) form or as a continuous layer (petroplinthite), also referred to as ironstone. Soils with petroplinthite are especially abundant in the transition zone from rain forest to savannah. Plinthite concretions can also occur as a dense layer of nodules known as pisolites, often lying close to the surface due to the removal of the soil between the pisolites by termites for building their nests.

Typical Ferralsol from near Jimma, Ethiopia, displaying a characteristic deep, homogeneous, red profile lacking any distinct horizon features. (JD)

A clear example of the typical nut-shaped soil structure from a nitric horizon in Ethiopia. The dark red colour is indicative of a significant amount of clay and active iron. Such soils are associated with the weathering of basic rocks, such as basalts. (EM)

Plinthite cap on the soil surface in Ghana. Plinthosols are formed in low-lying locations where iron-rich water from adjacent uplands can accumulate, precipitate and harden. Exposed plinthite may ultimately lead to an inversion of the original relief. Over time, uncapped soil is removed by erosion, leaving the capped soil as the highest parts of the landscape. (EM)

Low and high activity clays

- Clay minerals are categorised by low or high activity, which describes their ability or capacity to retain and supply nutrients, such as calcium, magnesium, potassium and ammonium.
- This is known as the soil's cation exchange capacity (CEC).
- High activity clays have a high CEC due to their large surface area. Generally, such soils are not highly weathered and have a high CEC under all pH levels.
- By contrast, low activity clays are more weathered. Consequently, due to their reduced surface area, they have a lower capacity to retain and supply nutrients and, depending on the pH of the soil, tend to supply phosphate, sulphate and nitrate, rather than base cations.

Soils with an argic horizon and low or high activity clays

As described in the previous pages, clay particles in the soil can be moved from one layer to another, giving rise to a subsurface horizon with a higher clay content than the overlying horizon.

Three common soil types occur in the humid tropics displaying clay-rich subsurface horizons:

- strongly acidic soils that develop in the weathering products of aluminium-rich metamorphic rocks, or where the weathering of secondary high-activity clay minerals, such as vermiculite or smectite produce high levels of aluminium, referred to as Alisols. Such soils are most common in old land surfaces with a hilly or undulating topography under humid tropical or monsoon climates. High levels of aluminium in the subsoil give the soil a reddish colour and can hinder biological activity
- strongly acidic soils that develop on the weathering products of acidic parent material (which give rise to an accumulation of low activity clays) in old land surfaces with a hilly or undulating topography under humid tropical climates are referred to as Acrisols. Acrisols generally exhibit a strong yellow- to red-coloured argic horizon overlain by a much lighter (whitish to yellow) bleached horizon
- where the climate has a pronounced dry season and the soils on old erosional or depositional surfaces are enriched in base cations through different processes (e.g. aeolian dust, biological activity, etc.), the resulting soils are known as Lixisols. Usually, the soil overlying the clay-rich horizon has a notably coarser texture. Many regard these soils are 'fossilised', reflecting a more humid climate

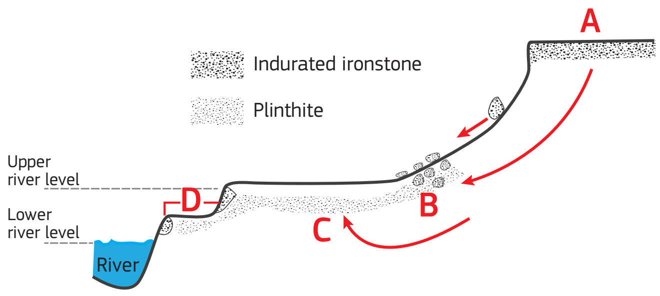


Figure illustrating the four distinct landscape positions where plinthite and ironstone occur. (LJ)

A: indurated ironstone (massive iron pan or gravel) capping an old erosion surface. Ironstone caps form a shield against erosion. The result is an inversion of the original relief where parts that initially were the lowest of the landscape become the highest

B: plinthite and ironstone (gravel and boulders) in a colluvial footslope (subject to iron-rich water)

C: plinthite in soils of a low-level plain (river terrace) with periods of high groundwater

D: along the banks of rivers where plinthite becomes exposed and hardens to ironstone

Why are rocks acid or basic?

- The terms 'acidic' and 'basic' are often used to describe igneous rocks or related parent material of soils.
- However, this does not refer to the pH of the material but rather to the amount of silica in proportion to Mg, Fe and Ca.
- Igneous rocks that contain significant amounts of silica (at least 66 % SiO_2 by mass, which normally occurs as quartz) are referred to as acid. Examples include granite and rhyolite.
- Conversely, the term 'basic' is applied to rocks containing dark minerals such as olivine, plagioclase and biotite. Rich in Mg, Fe and Ca but with relatively low amounts of silica. Examples include basalt, dolerite and gabbro.
- Recently, the term 'mafic' is used in place of basic while felsic is used for acid. Intermediate rocks (e.g. andesite) contain roughly even mixtures of felsic and mafic minerals.

Common processes in a dry tropical/subtropical climate

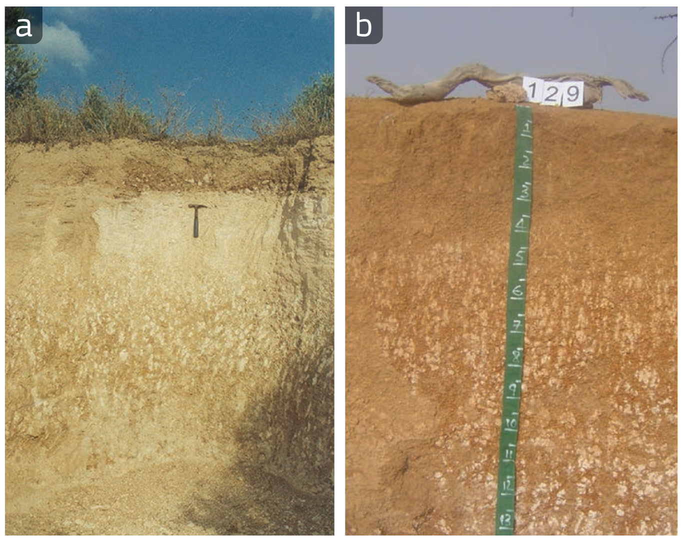
Where precipitation is lower than evapotranspiration and high temperatures cause groundwater to rise to the surface, several distinctive soil types can occur. These include:

Soils with accumulations of calcium carbonate

One of the most widespread soil-forming processes in dry climates involves the movement of calcium carbonate ($CaCO_3$) from surface horizons to an accumulation layer at some depth (a process referred to as secondary accumulation). On wetting (such as after rainfall), lime dissolves allowing calcium and bicarbonate ions (Ca^{2+} and HCO_3^-, respectively) to move downwards with the percolating soil water. When the water eventually evaporates, calcium carbonate precipitates as calcite where the percolation stopped. Calcite is not evenly distributed throughout the soil matrix. Root channels and wormholes act as channels along which the solution can flow, allowing the calcite to precipitate on the channel walls. When narrow root channels become filled with calcite, the resulting cast-like shape of the root is known as pseudomycelium. Other characteristic forms of calcium carbonate accumulation are soft or hard lime nodules and platy or continuous layers know as calcrete or hardpan. Calcite 'beards' can be found as pendants below pebbles. In eroding land, lime concretions may occur right at the surface of the soil.

Soils with accumulations of gypsum

Gypsum ($CaSO_4{\cdot}2H_2O$) dissolved from gypsiferous parent materials is moved through the soil by water and, in a similar manner to calcium carbonate, is precipitated in an accumulation layer when the water is removed. Where soil moisture moves predominantly upward (i.e. where a net evaporation surplus exists for an extended period each year), a gypsum-rich horizon occurs within the soil body. Gypsum is also leached from the surface soil in wet winter seasons and re-accumulates deeper in the soil as a loose, powdery substance. Over time, gypsum crystals may cluster together as compact layers or surface crusts that can become tens of centimetres thick. Gypsum can precipitate in former root channels (gypsum pseudomycelium), in voids, as coarse crystalline gypsum sand or in strongly cemented horizons (petrogypsic). In places, it forms massive crystalline structures known as desert roses.



(**a**) A profile of a calcium carbonate-rich soil from the Mediterranean. The white material around the hammer is a dense calcite horizon. Much of the free lime in the topsoil has been leached out, giving it a darker appearance. (**b**) A soil exhibiting secondary accumulation of gypsum. The upper part of the profile is almost completely lacking in gypsum, has very low organic matter and a weak, sub-angular blocky structure. Below 40 cm, the gypsum has precipitated along vertical cracks in the soil. (TG, RV)

A duric horizon from South Africa containing rounded or sub-angular durinodes. These indurated accumulations of silicon dioxide are hard and brittle. (EM)

Detail of desert rose, the common name given to rosette formations of gypsum with sand inclusions. The rosette shape tends to occur through the formation of crystals during the evaporation of shallow salt lakes in arid sandy conditions. (DAL)

Soils with accumulations of silica

In many arid regions (although not exclusively), soils known as Durisols contain very hard layers of silica-enriched materials in the subsoil. These materials range from silica-cemented sand and gravel to a nebulous matrix enriched with small silica particles. The conditions under which such features develop are uncertain as nearly all occurrences are 'fossil' because such soils do not seem to be forming extensively at present. Theories include the precipitation from silica-rich groundwater in arid/semi-arid climates or by intense weathering in a warm, humid climate.

Soils with lower levels of gypsum and calcium carbonate in the upper 30 cm soil layer can support grazing and some drought-tolerant crops when carefully irrigated. The hard duripan material is commonly used for road construction.

Soils with accumulations of salt

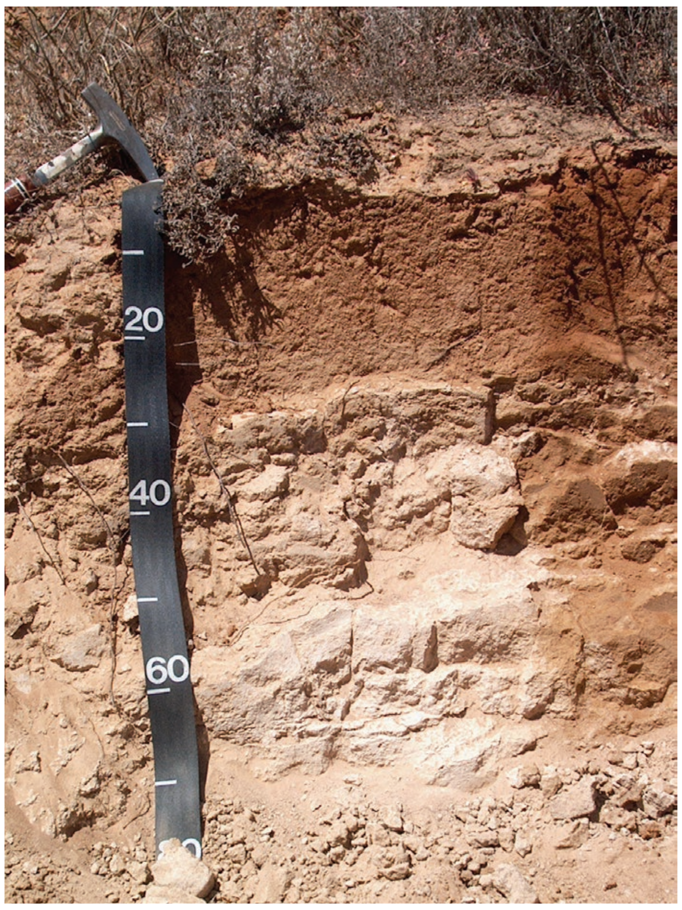
A soil is regarded as saline if the salt concentration is around 2 500 parts per million (ppm). Soils affected by soluble salts or by their ions are typical of semi-arid and arid regions and cover about 6.5 % of the Earth's surface. Soluble salts can be released through the weathering of rocks or because the parent material contains high levels of salt (e.g. old marine sediments or evaporation deposits). However, the majority of salt-affected soils develop where saline groundwater rises to the surface and dissolved salts accumulate in the soil due to evaporation. Salts can also be carried into depressions in the landscape by saline surface water flowing from higher ground. In dry lands, salinity can occur even when the water table is two or three metres from the surface of the soil. The main ions responsible for salinisation are Na^+, K^+, Ca^{2+}, Mg^{2+}, SO_4^{2-} and Cl^-.

Depending on the chemical composition, the reaction between the soil and salts may differ. Salts containing sodium (Na^+) cause organic compounds to become mobile and are eventually leached out of the topsoil, resulting in the development of a bleached horizon. The pH of such soil types is typically above 9.

Salts in soil can also result from irrigation, since almost all water (even natural rainfall) contains some dissolved salts. When crops use the water, these salts are left behind in the soil and accumulate over time. They must be artificially leached or flushed out of the root zone by applying additional water. Salinisation can be increased through poor drainage or use of saline water for irrigation. Saline soils also occur in ephemeral or closed basin lakebeds, also referred to as salt pans, salt flats, sebkhas, playas or chotts.

Strongly saline soils with high concentrations of soluble salts are known as Solonchaks, while soils with dense, clay- and sodium-rich subsoils are known as Solonetz.

Salt efflorescence (aluminium and/or iron sulphate) on the surface of a wet, lowland soil. In the past, this area was used for rice cultivation but is now abandoned. (JPM/IRD)



A soil profile from Namibia which has formed by the evaporation of groundwater containing high levels of sodium bicarbonate. The topsoil does not exhibit any well-defined horizons, and a salt crust has developed on the surface. (EM)

Soil-forming processes

Common processes in cold climates

In very cold environments, such as those found in high latitudes and elevations, the soil temperature may be below 0°C for much of the year, which means that water in the soil occurs mostly as ice, and permanently frozen ground is common. The upper part of the soil may only thaw during the short summer months. In these conditions, physical weathering through frost shattering and cryoturbation (mixing of the soil as a result of freezing and thawing cycles) is highly evident.

The presence and mobility of unfrozen soil water is a key factor as it migrates along the thermal gradient toward the freezing front in the soil. Specific cryogenic processes that affect soil formation are frost heave (where soil material is lifted), churning, sorting and orientation of soil materials, thermal cracking, surface cementing and the build up of ice either as crystals, massive layers or as wedges. These cryogenic processes give rise to very distinctive soils and surface features referred to as patterned ground. In addition, many of the soil processes described in the preceding pages (accumulation of organic matter, leaching, clay movement and destruction) can also be found. Despite the presence of ice, these soils during the summer months still provide the rooting media, nutrients and water for plants and biological life in these extreme ecosystems.

Summit of Mount Everest, the world's highest peak. Cold conditions favour cryogenic process in the soil. (GH)

Common processes on volcanic materials

Soils that develop from ejected volcanic materials such as ash, tuff, pumice, cinders and lava often contain high proportions of volcanic glass. Chemical weathering of primary minerals and volcanic glass leads to the formation of secondary aluminium- and silica-rich minerals, such as allophane and imogolite (under high rainfall) or halloysite (where rainfall is lower). The weathering process liberates aluminium (Al^{3+}) ions, which become tied up with humus in stable Al-organic compounds as the aluminium protects the organic material against biodegradation. Any free ferric iron (Fe^{3+}) usually precipitates as ferrihydrite (a form of iron oxide).

Such poorly crystalline materials have a large surface area and, consequently, can absorb large amounts of water. However, due to their high anion exchange capacity, such materials have a low ability to retain and supply nutrients, and therefore require very large additions of phosphorus to stimulate higher crop yields.

The classic volcanic cone of Ol Doinyo Lengai in Tanzania. By and large, volcanic soils are very fertile, especially on intermediate or basic volcanic ash that is not exposed to excessive leaching. The strong affinity of iron and aluminium (and their oxides) to remove compounds such as phosphorous from the soil solution in a form that makes them unavailable to plants (a process known as sorption) can be a significant problem that requires the application of lime, organic material or phosphate fertiliser. Volcanic soils are easy to till, have good rootability and water storage properties. (EM)

Soils conditioned by water

When it rains, water percolates through the soil and, in many cases, drains away. However, in some places the soil texture or the presence of an impermeable barrier prevents water from escaping, causing pores and cavities to become full of water (also referred to as groundwater). In some soils, groundwater can be found at relatively shallow depths (< 2 m). This situation generally exists due to a slowly permeable substrate, depressions in the landscape, which collect water, or in marshy areas near to the coast.

The presence of a shallow groundwater table strongly decreases the movement of gases in the soil because oxygen and carbon dioxide diffusion in waterlogged pores is very slow compared to air-filled pores. If organic matter is present in the waterlogged soil, the metabolic activity of the microorganisms creates an oxygen deficit and a state known as 'reduction' develops. In these conditions, ferric iron is converted to the more soluble, and therefore mobile, ferrous iron (Fe^{2+}). While ferric oxides are responsible for giving subsoils their characteristic yellowish- or reddish-brown colours, their disintegration into ferrous oxides gives the soil a distinctive greyish or bluish colour. However, in some of the larger pores where some oxygen may remain, mottles of rust-coloured material indicate the redeposition of ferric oxides. In soil science, two basic types of waterlogged soils are recognised, surface water and groundwater gley.

This soil is a well developed surface water gley. After rain has fallen, water is held periodically (a state known as stagnant) above an impervious clay-rich horizon (below 40 cm in the photograph). In periods with a precipitation surplus, stagnant water can appear on the surface but will disappear when the soil dries out. This soil is characterised by the presence of grey ped surfaces and root channels, while the interior of the peds are enriched by ferric iron. (EVR)

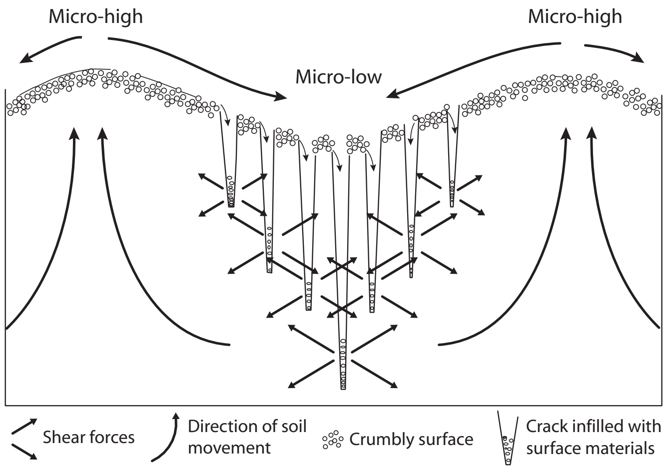
Soils that develop in river (fluvial), lake (lacustrine) and marine (associated with the sea) sediments have a number of distinctive characteristics. The soils of these environments display evidence of stratification (layering) which reflects deposition of the parent material in water. These soils are also subject to periodic flooding, which brings in additional sediments, organic matter and nutrients. Such soils tend to occur on alluvial plains, river fans, valleys and tidal marshes (including mangroves). The horizontal strata of the fertile loamy sediments are very evident in this image. Changes in colour reflect specific flood events or past soil development. (JD)

Soils conditioned by the presence of swelling clays

In areas with distinct dry and wet seasons and where the parent material contains large quantities of swelling clay minerals known as smectites, soils are characterised by the presence of deep cracks in dry periods which close in the wet season. The closure of the cracks is driven by the expansion of the smectite minerals as they absorb water. Such soils are also defined by the presence of characteristic structural aggregates (spheroids).

Shrinkage of the clay on drying leads to the formation of cracks. In addition, the surface breaks up into granules or crumbs that can fall into the cracks. When the soil is rewetted, part of the space that the soil requires for its increased volume is occupied by the granular material in the cracks, which results in the build up of shear stress within the soil material. Continued pressures through the uptake of more water eventually cause the soil masses to shear and slide against each other.

The shear planes are known as slickensides and display polished surfaces that are grooved in the direction of force causing the movement. Intersecting shear planes produce wedge-shaped angular blocky peds that tend to increase with depth (probably reflecting the moisture gradient). This internal movement of soil, coupled with the deposition of surface crumbs in deep cracks, means that the subsurface soil is pushed towards the surface and mixed. This process is known as churning or pedoturbation. This constant mixing of the soil material results in an extremely deep A horizon. Such soils tend to develop either at the foot of slopes or on plains as a result of the weathering of basalt or redeposition of smectite-rich lacustrine sediments.



A simplified view of the processes operating in soils with swelling clays. During dry periods, the clays shrink, causing cracks to open in the soil surface. Over time, crumbs from the surface fall into the cracks. On wetting, clays in the soil body expand, causing the cracks to close. However, the newly buried surface material causes internal stresses which leads to a mixing of the soil body. This churning often creates a distinctive micro-relief known as gilgai, where the land surface becomes irregular with alternating mounds (puffs) and depressions (hollows). (MF)

Pasture on a soil with swelling clays from the Gonder Region, Ethiopia. The characteristic gilgai microrelief is evident through the dark and light colours of the grass. The darker regions indicate slight depressions. (JD)

The effects of living organisms

One of the most important factors affecting soil processes are living organisms. Increasingly, biological activity is being recognised as an important factor in regulating soil processes, such as storage of carbon, and thus soil profile development. The role that living organisms play in soil development cannot be overstressed. The accumulation and decay of organic matter, the development of soil structure, the mixing of soil material (bioturbation), nutrient cycling, the physical breakup of bedrock by roots and the bacterial destruction of clay minerals are all the result of organisms living in the soil, and are critical soil-forming processes.

In a broad sense, the activity of organisms in the soil is closely linked to climate. Nevertheless, biological activity is also present in hot, dry desert regions (see page 87). In low temperatures or in very wet conditions, bacterial decomposition is reduced and organic matter accumulates. In the warm and wet conditions of the tropics, both bacterial and fungal activity are intense.

In temperate zones, burrowing mammals, beetles and earthworms can have a strong influence on soil processes by facilitating the transfer of water and air along burrows and channels. In the tropics, termites and ants play a major role in nutrient recycling and the redistribution of soil material – the movement of particles of subsoil to the surface by termites is one of the main factors responsible for the homogenised profiles that are typical of some tropical soils.

Organic vs. mineral soils

- Soil material is referred to as organic if it contains more than 20 % organic matter.
- Mineral soils, by contrast, contain less than 20 % organic matter but can possess organic surface horizons.

Soil organic matter is derived from the remains and exudates of living organisms (predominantly plants). Organic matter is utilised by a variety of soil organisms as both a source of energy (to function) and materials for building their bodies. During this process, water, carbon dioxide (CO_2) and various organic compounds such as sugars, starches, proteins, carbohydrates, lignins, waxes, resins and organic acids, are converted through a process known as mineralisation, into inorganic compounds, such as ammonium (NH_4^+), phosphate (PO_4^{3-}) and sulphate (SO_4^{2-}). This process, together with the release of CO_2 from the soil, is vital for plant growth. Some of these compounds are immobilised by being incorporated into the bodies of soil organisms, and are only available after the death of the organism.

The annual return of plant and animal residues to the soil varies with climate, vegetation type and land use. The effect can be easily seen when comparing soils of grasslands and forests. The organic matter content, moisture-retention and nutrient-holding capacity of grassland soils are generally much higher than those of forests. In addition, the type of vegetation can also affect soil characteristics. The litter of coniferous trees tends to be low in calcium, magnesium and potassium, which tends to lead to acidic conditions in the soil. Conversely, soils under natural grasslands favour nitrogen fixers, such as *Azotobacter* (see page 33).

Tropical rainforests generally return about 15 tonnes of litter per hectare each year, compared to around eight tonnes for temperate grasslands, two tonnes for agricultural soils and 0.1 tonnes for alpine forests. Root decay contributes a further 30 - 50 % of the amount produced from leaf fall.

Soil organic matter and carbon

- Carbon is an important constituent of all living matter.
- All soils contain varying amounts of the element carbon (C) in both organic and inorganic forms.
- The term soil organic matter (SOM) is used to describe the organic constituents in the soil (e.g. cells and tissues of soil organisms and plant and animal residues at various stages of decomposition).
- With the exception of calcareous soils, the majority of C in soils is held as organic carbon (OC).
- The term 'soil organic carbon' refers to the C occurring in SOM.
- On average, 58 % of SOM is carbon.
- Living organisms play a key role in the C cycle (see page 104).

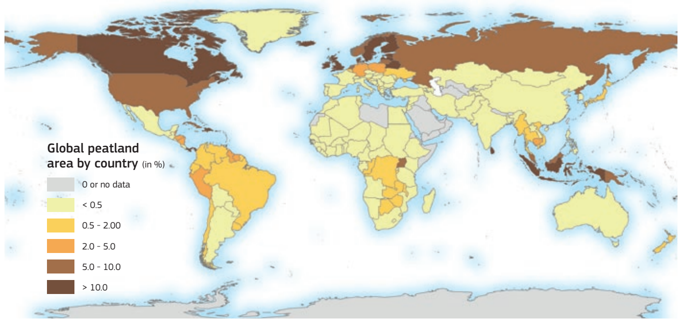
Peat formation

Peat is a dark, unconsolidated, organic-rich material that has developed when the decay of plant material is slowed as a result of a lack of oxygen in waterlogged (anaerobic) conditions. Such conditions are found in wetlands such as bogs, fens, moors, mires or swamps. Three main types of peat are recognised: sapric (very decomposed, hardly any recognisable plant fibres), hemic (moderately decomposed) and fibric (slightly decomposed).

Peat can also accumulate in tundra and mountain environments where temperatures are low enough to slow down decomposition. In soil classification, organic soils are known as Histosols (from the Greek *histos*, meaning tissue).

Peat accumulates slowly. Globally, peatlands are distributed very unevenly, with North America accounting for around 44 % of the total area. Most of the remaining peatland is found in Asia (28 %) and Europe (24 %). Approximately 95 % of the world's peatlands are found in the Northern Hemisphere. Peat is the initial stage of coal formation.

Soils saturated with water and cool, humid conditions lead to peatland formation. This plant is *Eriophorum angustifolium*, commonly known as common cotton grass or bog cotton – a species of sedge often found on peat soils in North America, North Asia and Northern Europe. (AJ)



Global distribution of peatlands (derived from Parish *et al.*, 2008). (RP, UNEP/GRIDA) [22]

Wetlands

- Most people are unaware of the subtle differences in the names of different wetland environments (also known as mires):
  - bogs – water only by precipitation (known as ombrotrophic). Acidic conditions, low nutrients, predominantly grasses, heath and moss;
  - fens – mostly mineral-rich surface or groundwater (known as minerotrophic). Less acidic, higher nutrient levels and more diverse plant community than bogs;
  - swamp – wetland with trees, often along rivers or lakes. Slow-moving to stagnant fresh, brackish or seawater;
  - marsh – often found at the edges of lakes, streams and estuaries where they form a transition between the aquatic and terrestrial ecosystems. They are often dominated by grasses, rushes or reeds.

Litter layer on the floor of a rainforest. Rapid decomposition due to high temperatures and humidity levels leads to a dark-coloured surface soil. (TAT)

Soil formation driven by human activity

Some people argue that all cultivated soils have been affected or altered by human activity through the mixing of topsoil and subsoil by ploughing, changing the chemical balance through liming, or depleting nutrients through intensive farming. However, there are numerous examples throughout the world where the entire soil body was either totally formed, or at least profoundly modified, through human activities, such as the addition of organic materials or household wastes, irrigation or cultivation. Collectively known as Anthrosols, examples include:

- very deep tillage that is below the depth of normal ploughing – often through the use of terraces
- intensive fertilisation with organic fertilisers such as manure, kitchen refuse, compost, human excrement
- continuous application of earth (e.g. sods, beach sand and shells) or sediment through irrigation
- wet cultivation that involves puddling the surface of the soil or human-induced wetness (e.g. paddy fields for rice cultivation)

Another major human management factor is drainage which affects the frequency and duration of periods when the soil is saturated by water. In waterlogged soils, drainage can allow crops to be grown by allowing oxygen to move within the soil. The drainage of peatlands for cultivation can eventually result in total soil loss from shrinkage and wind erosion if the peat is allowed to dry out completely.

While not spatially extensive, soils that have been heavily modified by human activities are very important at a local scale. The profile above shows an Anthrosol from Belgium where sods (pieces of grass and the soil beneath it held together by roots) collected from heathland areas have been added to the original sandy soil (visible below 80 cm). The sods were put in a special container to compost and soak up nutrients. As evident from the dark colour, these soils still contain organic matter, several centuries after the practice has ended. After many years of such practices, the land surface may be raised considerably, as shown by the white lenses around a depth of 40 cm which is sand that collected in cultivation furrows in an earlier land surface. (SD)

Soil in sandy sediments

Soils that have developed in coarse material (> 0.063 mm) have poor cohesion and structure coupled with low water retention capacity and organic matter levels. In addition, sandy materials are often acidic. These factors affect soil formation. The most common constituent of sand is silica (silicon dioxide, SiO_2), usually in the form of quartz, which, because of its chemical inertness and considerable hardness, is the most common weathering resistant mineral. Iron impurities or staining can give the quartz crystals a deep yellow or red colour. While many arid regions are characterised by blown sand (predominantly quartz but other materials, such as gypsum, can dominate), sand can also be deposited by rivers and along coasts by waves and currents. Along desert margins, climatic fluctuations mean that dunes can be fixed by vegetation. In some cases, their aeolian nature is still obvious but in other situations, soil-forming processes can give rise to quite different soils.

Coarse sediments that develop as a result of intense and long-term weathering tend to be more angular compared to the rounded grains that have been transported by water or wind.

Map of global distribution of soils

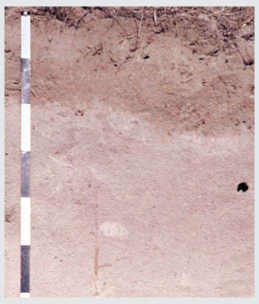
Climate plays an important role in soil formation. Hence, soils generally differ from one major climatic zone to another. Equatorial regions, with high temperature and rainfall levels, have deep, strongly weathered and very leached soils with low nutrient levels. More arid conditions, with low precipitation and high evaporation, produce soils containing easily soluble components such as calcium carbonate or gypsum. Soils in temperate climates tend to have more organic matter while the effects of parent material and precipitation levels are more evident. In cold climates, soil formation is restricted and strongly influenced by freeze-thaw processes and the presence of ice in the subsoil ('permafrost'). Past climates also play an important role in determining current soil distribution, especially in the subarctic and northern temperate regions where glaciers have removed all soil material and new soils were formed after the retreat of the ice. Consequently, soils of these regions are relatively young or 'immature'.

Soil classification schemes generally reflect different concepts of soil formation. The boxes on these two pages are simplified descriptions of the world's major soil types according to the World Reference Base for Soil Resources (WRB), an internationally used soil classification system. More information on the WRB system can be found at:

www.fao.org/soils-portal/soil-survey/soilclassification/world-reference-base/en/

Arenosols: from Latin ***arena***, sand

Developed as a result of *in situ* weathering of quartz-rich parent material or in recently deposited sands (e.g. dunes in deserts and beaches). Among the most extensive soil types in the world. Soil formation is often limited by a low weathering rate. Prone to wind erosion. (ISRIC)



Durisols: from Latin ***durus***, hard

Associated with old surfaces in arid and semi-arid environments. They display hardened accumulations of silica (SiO_2) in the soil. Durisols develop over long periods during which the soil reaction is so alkaline (pH > 8) that the silica becomes mobile. Regarded as 'fossil' soils. (FE)

Calcisols: from Latin ***calcarius***, lime-rich

Formed through the leaching of carbonates from the upper part of the soil which precipitate when the subsoil becomes oversaturated or by the evaporation of water which leaves behind dissolved carbonates. Found in dry climates. (EM)

Ferralsols: from Latin ***ferrum***, iron, and ***alumen***, alum

Mostly associated with high rainfall areas and very old land surfaces, they are strongly leached soils that have lost nearly all of their weatherable minerals over time. Dominated by stable products, such as aluminium/iron oxides, which give strong red and yellow colours. Nutrient poor. (SD)

Acrisols: from Latin ***acer***, acid

Strongly acid soils with a clay-enriched subsoil and low nutrient-holding capacity. Mainly found in the wetter parts of the tropics and subtropics. Normally associated with acidic bedrock and deficient in nutrients. Thus requiring substantial applications of fertiliser to produce satisfactory crop yields. (OS)

Cambisols: from Latin ***cambiare***, to change

Young soils, generally lacking distinct horizons or with only slight evidence of soil-forming processes usually through variations in colour, the formation of structure or presence of clay minerals. Globally extensive – characteristics dependent on the nature of the parent material. (ISRIC)

Fluvisols: from Latin ***fluvius***, river

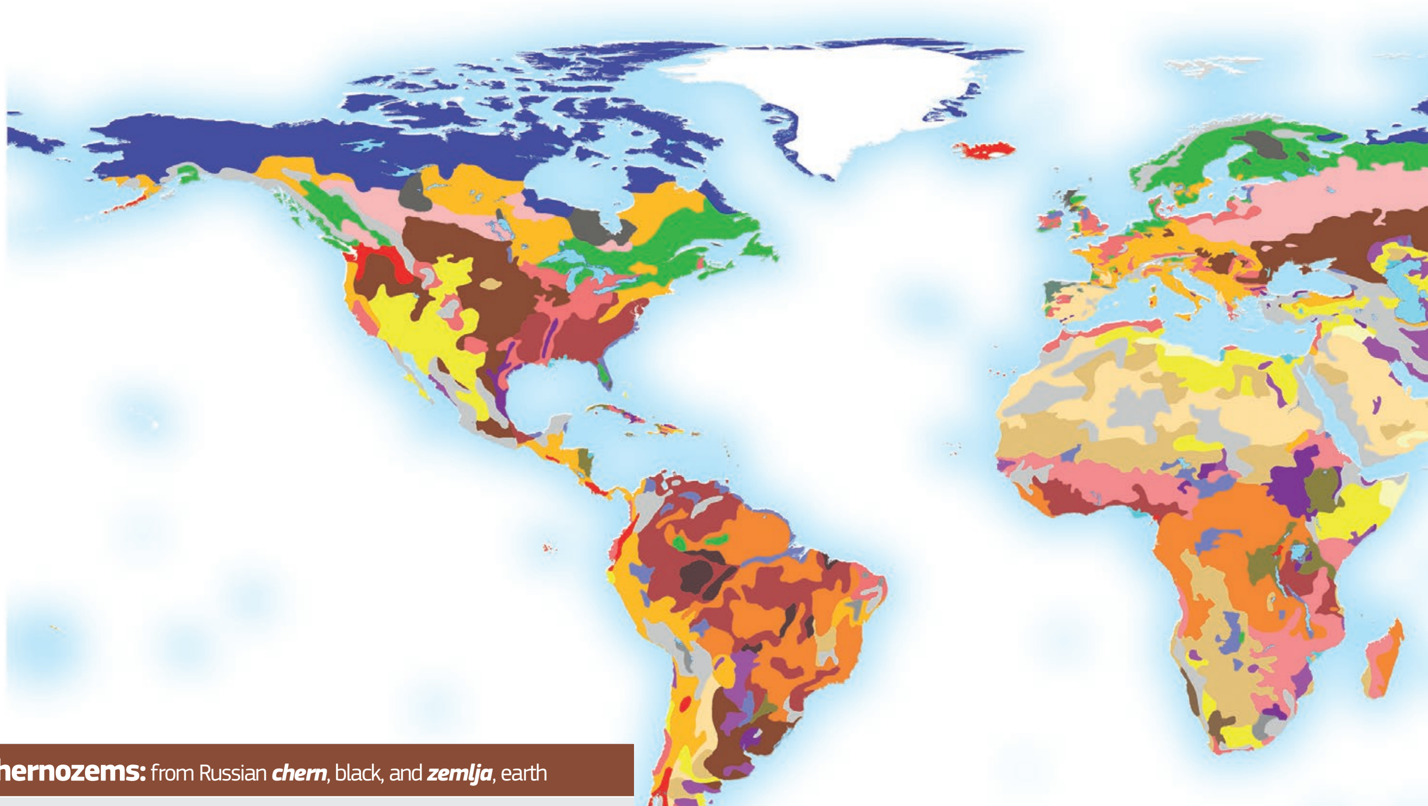
Occurring in all periodically flooded areas, such as flood plains, river fans, valleys, tidal marshes and mangroves. Fluvisols show a layering of sediments with pedogenic horizons as a result of deposition by water. Their characteristics depend on the nature and sequence of the sediments. (JD)

Albeluvisols: from Latin ***albus***, white, and ***eluere***, to wash out

Soils with a subsurface horizon that tongues into a horizon which has accumulated clay. Formed mostly in unconsolidated deposits on flat to undulating plains under coniferous or mixed forest in boreal and temperate climates with cold winters and short cool summers. (EM)

Alisols: from the Latin ***alumen***, aluminium

Very acid soils with a clay-enriched subsoil and high nutrient-holding capacity. Acidity is caused by the weathering of minerals which release a large amount of aluminium – often at levels that are toxic to most crops. They occur in humid tropical, humid subtropical and warm temperate regions. (ISRIC)



Andosols: from Japanese ***an***, black, and ***do***, soil

Soils developed from materials ejected from volcanoes (e.g. ash, pumice and cinder) which weather to produce specific clay minerals. In humid climates, many Andosols develop a thick, dark topsoil as a result of the fixing of organic substances by aluminium that is released from the weathering of the clay minerals. (ISRIC)

Chernozems: from Russian ***chern***, black, and ***zemlja***, earth

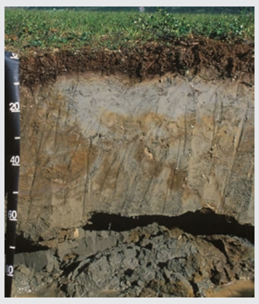
Soils with a very dark-brown or blackish surface horizon with a significant accumulation of organic matter and a neutral pH. Secondary calcium carbonate deposits occur within 50 cm of the lower limit of the humus-rich horizon. High biological activity. Typically found in grasslands in temperate climates. (EM)

Anthrosols: from Greek ***anthropos***, man

Soils that exhibit surface horizons that have been modified profoundly through human activities, such as addition of organic materials or household wastes, irrigation and cultivation. These include plaggen, paddy and oasis soils as well as the *Terra Preta do Indio* in Brazil. However, they are not evident due to the scale of the accompanying map. (JD)

Cryosols: from Greek ***kraios***, cold or ice

Soils from cold regions where permafrost is found. Water occurs primarily in the form of ice and cryogenic processes, such as freeze-thawing cycles, cryoturbation, frost heave and cracking, are the dominant soil-forming processes, often giving distorted horizons and/or patterned ground. (SB)



Gleysols: from Russian ***gley***, 'mucky mass'

Occurring in low-lying areas or depressions where groundwater comes close to the surface and the soil is saturated for long periods of time. Other than characteristic colours depending on whether oxygen is present, they display little soil development. Often found with wetland vegetation. (OS)

Gypsisols: from Greek ***gypsos***, gypsum

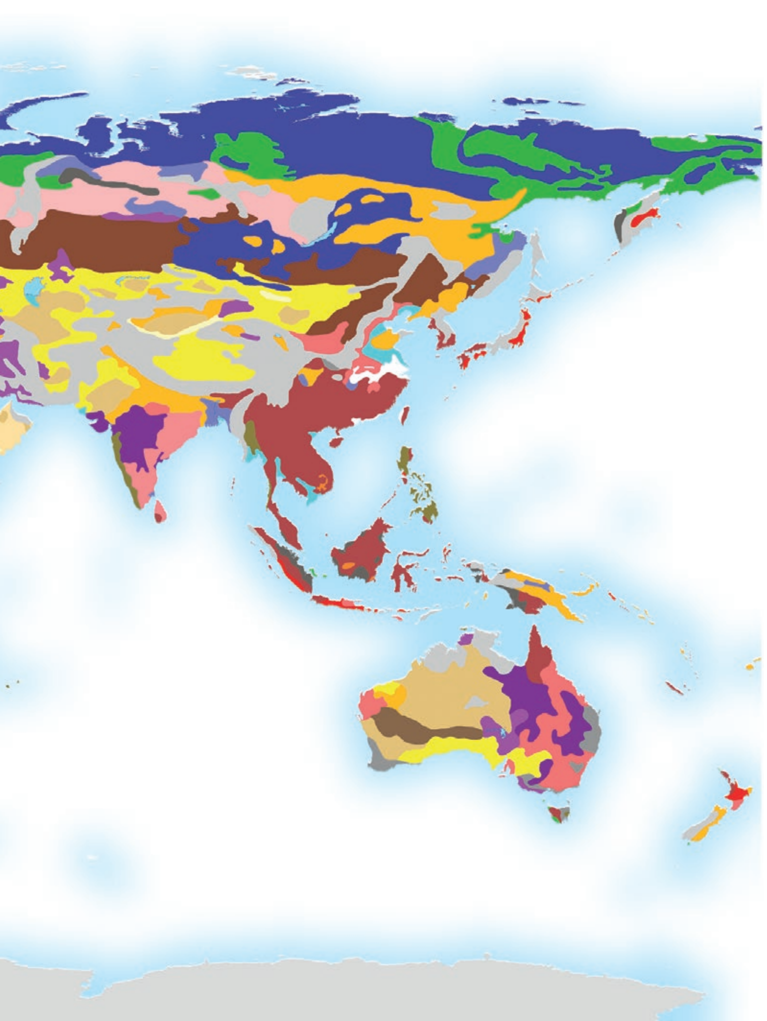
Similar to Calcisols, these are soils with secondary accumulations of gypsum ($CaSO_4{\cdot}2H_2O$). They are found in the driest parts of the arid climate zone and often reflect former lake beds that have dried up through evaporation. Vegetation is sparse xerophytic shrubs and grasses. (JD)

Histosols: from Greek ***histos***, tissue

Also known as peat, Histosols contain a high amount of organic matter (more than 20 %), have a high water content and very low bulk density. When drained, they suffer from irreversible shrinkage and subsidence. Found in wetlands and cold climates, which slow the rate of organic matter decomposition. (SD)

Kastanozems: from Latin ***castanea***, chestnut, and Russian ***zemlja***, earth

Soils with a deep, dark coloured surface layer with a significant accumulation of organic matter, high base saturation and presence of calcium carbonate in the subsoil. Found in drier parts of the grassland regions where leaching is low but sufficient biomass production to form the organic-rich surface layer. (SH)



Global distribution of the main soil types according to the WRB system. Colours on the map correspond to the colours on the soil name boxes around the map. (JRC) [23]

Leptosols: from Greek ***leptos***, thin

Shallow soils over hard rock, very gravelly material or highly calcareous deposits. Limited pedogenic development gives a weak soil structure. Globally present, especially in mountainous and desert regions where hard rock is exposed or comes close to the surface and weathering is active. (JD)

Lixisols: from Latin ***lixivia***, washed-out substances

Slightly acid soils that show a distinct increase in clay content with depth (predominantly kaolinite with limited capacity to hold nutrients). Found in the dry savannah regions with low biomass production, they have low organic matter content and lack a well developed soil structure. Prone to erosion. (EM)

Luvisols: from Latin ***luere***, to wash

Soils with a distinct increase in clay content with depth as a result of clay movement from the upper part of the soil to the lower part. The clay gives a high nutrient-holding capacity. In general, Luvisols have a well-developed soil structure, which contributes to a good water-holding capacity. (ISRIC)

Nitisols: from Latin ***nitidus***, shiny

Developed mainly from basic iron-rich rocks such as basalt in tropical climates. They have a dark red colour and a well-developed structure. The iron content is high, which enforces strong bonding of clay particles and the formation of the nut-shaped aggregates with shiny surfaces. (OS)

Phaeozems: from Greek ***phaios***, dusk, and Russian, ***zemlja***, earth or land

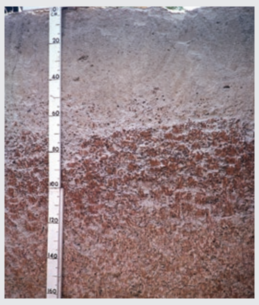
Soils with a thick, dark-coloured surface layer, rich in organic matter and nutrients. Their development requires a reasonable amount of precipitation and lush vegetation, preferably grasses. Similar to Chernozems and Kastanozems but more intensively leached. (ISRIC)

Planosols: from Latin ***planus***, flat

Soils with very low permeability in the subsoil which causes water entering the soil to stagnate above this layer. The transition to the low permeability layer is very abrupt and the clay content increases significantly. Most Planosols have a structureless topsoil due to the removal of iron in waterlogged conditions. (EVR)

Plinthosols: from Greek ***plinthos***, brick

Identified by the accumulation of iron (and manganese) in the subsoil as large mottles or concretion that develop under fluctuating groundwater. While buried, the layer (called plinthite) is soft and can be cut by a knife. However, once exposed to air and sunlight, it hardens irreversibly and becomes what is known as ironstone. (ISRIC)



Podzols: from Russian ***pod***, under, and ***zola***, ash

Soils with a distinctive ash-grey horizon which has been bleached by the loss of organic matter and iron oxides. This sits on top of a dark accumulation horizon of redeposited humus and/or reddish iron compounds. Typically occurring in humid temperate climates in coarse sand deposits. (AR)

Regosols: from Greek ***rhegos***, blanket

Soils in unconsolidated medium and fine-textured material showing only slight signs of soil development (e.g. some accumulation of organic matter producing a somewhat darker horizon). Similar to Arenosols (sand) or Leptosols (gravel). Soil development limited by low temperatures or aridity. (OS)

Solonchaks: from Russian ***sol***, salt

Strongly saline soils with high concentrations of soluble salts. Mostly associated with arid regions and areas where saline groundwater comes close to the surface. Their characteristics and limitations to plant growth depend on the amount, depth and composition of the salts. (AR)

Solonetz: from Russian ***sol***, salt, and ***etz***, strongly expressed

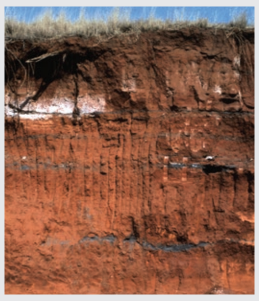
Strongly alkaline soils with a dense, columnar, clay-rich subsoil containing a high amount of exchangeable sodium, which has the ability to disperse clay particles and organic matter from the topsoil to the subsoil. Normally found in flat lands in climates with hot, dry summers or former salty coastal deposits. (EM)

Stagnosols: from Latin ***stagnare***, to flood

Soils with a perched water table, often caused by the presence of an impermeable barrier deep in the soil, leading to temporary water logging and the mobilisation of iron and/or manganese. This process gives rise to a characteristic colour pattern. Commonly referred to as pseudogley. (RS) – not visible due to the scale of the map.

Technosols: from Greek ***technikos***, skilfully made

Soils containing man-made artefacts (e.g. household or industrial waste), material that has been brought to the surface (e.g. mine dumps, oil spills) or soils sealed by an artificial surface (e.g. roads, hard-standing areas). Often contain toxic material. (OS) – not visible due to the scale of the map.

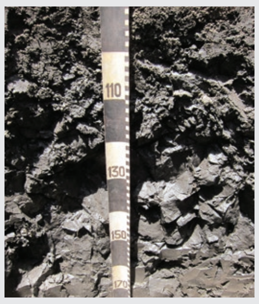


Umbrisols: from Latin ***umbra***, shade

Soils with a deep, dark-coloured surface layer that is rich in organic matter but has a low nutrient content. They are mainly associated with acid parent materials and areas with high rainfall. Umbrisols are the counterpart of nutrient-rich soils with a dark surface horizon (e.g. Chernozems and Phaeozems). (EM)

Vertisols: from Latin ***vertere***, to turn

Clayey soils that exhibit cracks which open and close upon drying and wetting due to the presence of the clay mineral, montmorillonite. This process brings material from the surface into the subsoil, giving rise to a 'churned' soil. Typically found in lowland areas that are periodically wet. (EVR)



Soil is by far the most biologically diverse part of the Earth. Soil biodiversity reflects the mix of living organisms in the soil. These organisms interact with one another and with plants and small animals, forming a web of biological activity. The soil food web includes earthworms, spiders, ants, beetles, collembolans, mites, nematodes, fungi, bacteria and other organisms. (VG, SA, EDM, CHB, MH, MR/KH, MBE, CA/KC, LT)

Introduction

Soil is one of the most diverse habitats on Earth. Nowhere in nature are species so densely packed as in soil communities. For example, a single gramme of soil may contain millions of individuals and several thousand species of bacteria. The complex physical and chemical nature of the soil, with a porous structure, immense surface area and extremely variable supply of organic materials, food, water and chemicals, provides a range of habitats for a multitude of organisms. These range from macro- to micro- levels depending on climate, vegetation and physical and chemical characteristics of a given soil. The species numbers, composition and diversity in a particular ecosystem depend on many factors including temperature, moisture, acidity, nutrient content and the nature of the organic substrates.

Soil biota includes archaea, bacteria, protists, tardigrades, rotifers, nematodes, acari (mites), collembolans (springtails), worms (enchytraeids and earthworms), macroarthropods (e.g. ants, termites, centipedes, millipedes, woodlice, etc.) and burrowing mammals. It also includes plant roots, fungi and lichens. Root exudates attract a variety of organisms that either feed directly on these secretions or graze on the microorganisms concentrated near the roots, giving this busy environment the name 'rhizosphere'. There are also animals, such as beetle larvae, flies and butterflies, that use the soil as a temporary habitat to reproduce or to spend their early life stages feeding on different live and dead plant materials until they reach their maturity. Soil communities are so diverse in both size and numbers of species, yet they are still extremely poorly understood and in dire need of further assessment. Research has been limited by their immense diversity, their small size and the technical challenge of identifying them.

Carl Linnaeus, also known after his ennoblement as Carl von Linné, is recognised as the father of modern taxonomy. (AZ)

Organisms can be classified in different ways. Taxonomy (from Ancient Greek τάξις *taxis*, 'arrangement' and -νομία *-nomia*, 'method') is the science of defining groups of biological organisms on the basis of shared characteristics and giving names to those groups. The rank-based method of classifying living organisms we use today was originally popularised by Swedish botanist Carl Linnaeus (1707-1778). In his landmark publication '*Systema Naturae*' (first edition published in 1735), Linnaeus used seven taxonomic ranks to classify 10 000 species of organisms: kingdom, phylum, class, order, family, genus and species. Other ranks and sub-ranks have been added over the years, with frequent discussions among taxonomists.

The greatest innovation of his system is the general use of binomial nomenclature (i.e. the combination of a genus name and a second term), which together uniquely identify each species of organism within a kingdom. Both names use Latin grammatical forms and they must be written in italics, or underlined when handwritten. Furthermore, in modern usage, the first letter of the first part of the name, i.e. the genus, is always capitalised in writing, while the specific epithet is not. For example, the human species is identified by the name *Homo sapiens*. When the specific name cannot be identified, the abbreviation 'sp.' is used to accompany the genus name (e.g. *Lumbricus* sp.). The abbreviation 'spp.' (plural) indicates 'several species' in that particular genus (e.g. *Agaricus* spp.). These abbreviations are not italicised (or underlined).

Soil biodiversity consists of organisms ranging from micro- to macro- body size. (**a**) Bacteria, (**b**) fungi and (**c**) protists represent examples of soil microorganisms; (**d**) nematodes are examples of soil microfauna; (**e**) collembolans represent an example of soil mesofauna; (**f**) myriapods and (**g**) earthworms are examples of soil macrofauna; (**g**) moles represent an example of soil megafauna. (WVE, EDM, SA, DR, AM, MH, DOH, SE)

Introduction

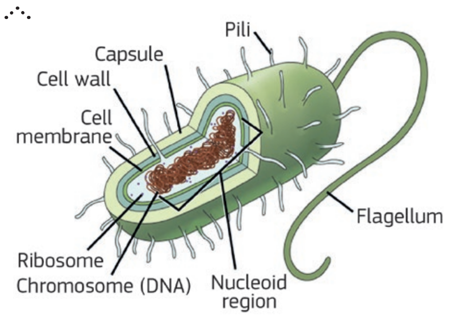
When Linnaeus developed his classification system, there were only two kingdoms, Vegetabilia (plants) and Animalia (animals). The advances in microscopy and staining techniques led to the identification of new organisms and a better understanding of cell structure and functioning. Although a general consensus has not yet been reached on how many kingdoms there are, all proposed classification schemes are based on three main criteria: cell type (prokaryote without a membrane-bound nucleus – *karyon* – or eukaryote with a nucleus and other organelles enclosed within membranes); the number of cells in the body (single cell or multicellular); and the ability to obtain food (autotroph or heterotroph).

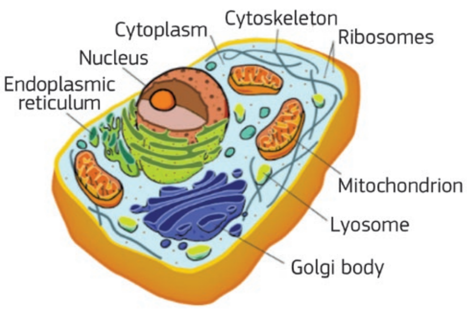
From around the mid-1970s onwards, there was an increasing emphasis on comparisons of genes on the molecular level (initially ribosomal RNA genes – see box below) as the primary factor in classification (i.e. genetic similarities among organisms). Accordingly, taxonomic ranks, including kingdoms, were to be groups of organisms with a common ancestor, and based on RNA studies the Linnaean categories have been updated to include 'Domain' as the highest rank in the taxonomic hierarchy. Therefore, although plants, fungi and animals may look different, they are more closely related to each other than they are to either the Bacteria or Archaea, which represent two different domains.

Linnaeus	1735	2 kingdoms	Animalia	Vegetabilia						
Haeckel	1866	3 kingdoms	Animalia	Plantae		Protista				
Chatton	1925	2 empires	Eukaryota						Prokaryota	
Copeland	1938	4 kingdoms	Animalia	Plantae		Protista			Monera	
Whittaker	1969	5 kingdoms	Animalia	Fungi	Plantae	Protista			Monera	
Woese *et al.*	1977	6 kingdoms	Animalia	Fungi	Plantae	Protista			Archaebacteria	Eubacteria
Woese *et al.*	1990	3 domains	Eucarya						Archaea	Bacteria
Cavalier-Smith	1993	8 kingdoms	Animalia	Fungi	Plantae	Chromista	Protozoa	Archezoa	Archaebacteria	Eubacteria
Cavalier-Smith	1998	6 kingdoms	Animalia	Fungi	Plantae	Chromista	Protozoa		Bacteria	
Ruggiero *et al.*	2015	7 kingdoms	Animalia	Fungi	Plantae	Chromista	Protozoa		Archaea	Bacteria

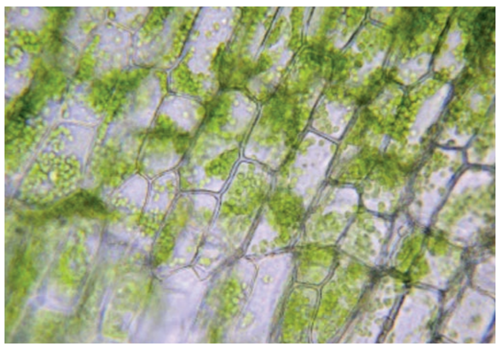
Since ancient times, scientists have been trying to classify living organisms. By the end of the 20th century, the English biologist Thomas Cavalier-Smith, after intense study of protists, created a new model with six kingdoms. During the 21st century, a phylogenetic approach, based on DNA comparisons (see box below), to classify organisms has gained strength. However, the real evolutionary relationship among eukaryotes, in particular protists (see page 31), is still debated and future changes in the classification might be needed. (JRC)

Prokaryotic cell	Eukaryotic cell
All the intracellular water-soluble components (proteins, DNA and metabolites) are located together in the cytoplasm enclosed by the cell membrane, rather than in separate cellular compartments.	The cytoplasm accommodates membrane-bound organelles, especially the nucleus, which contains the genetic material, and is enclosed by the nuclear envelope.





Unicellular	Multicellular
Also known as a single-celled organism, is an organism that consists of only one cell.	Organisms that consist of more than one cell.



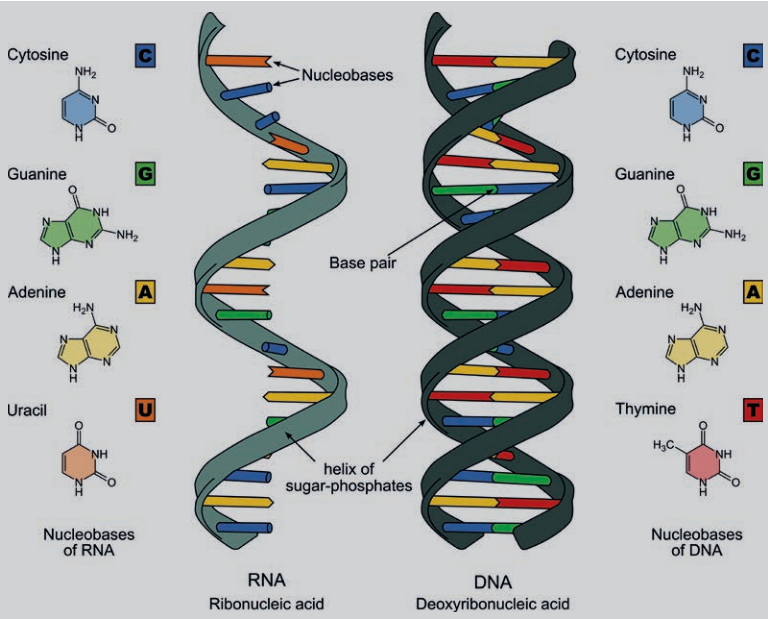
Autotroph	Heterotroph
"Self-feeding" organism that produces complex organic compounds (such as carbohydrates, fats and proteins) from simple substances present in its surroundings, generally using energy from light (photosynthesis) or inorganic chemical reactions (chemosynthesis).	Organism that cannot fix carbon and uses complex organic substances produced by, or available in, other organisms.

Three main schemes to classify living organisms. Based on the cell type an organism can be prokaryotic (without a nucleus) or eukaryotic (with a nucleus). According to the number of cells, an organism can be unicellular or multicellular. Depending on the ability to obtain food an organism can be classified as autotroph (able to produce food by itself) or heterotroph (cannot synthesise its own food). (EDM, DAT, ARDS, MG, MJIB, JRC)

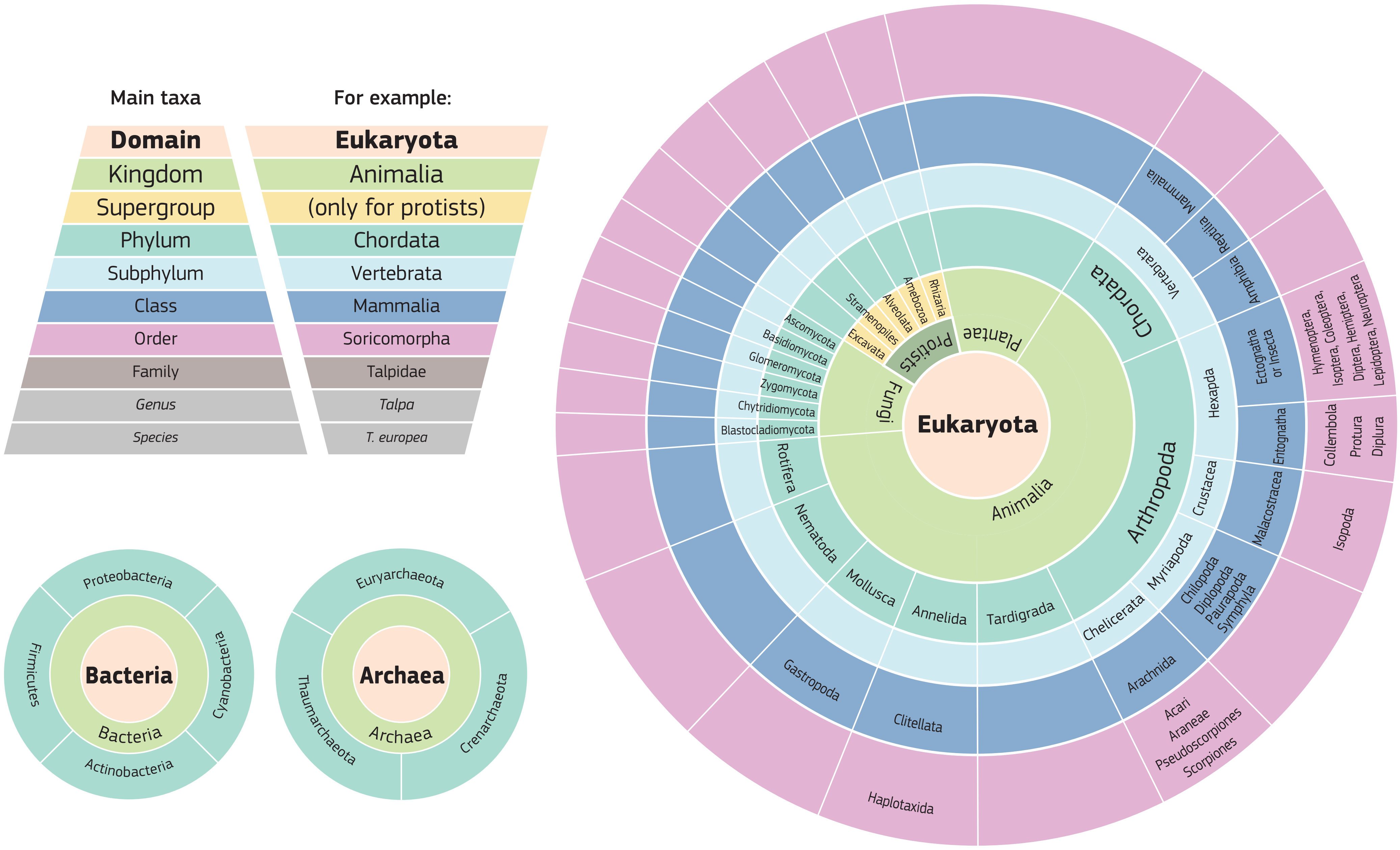
Contrary to popular belief, DNA was first isolated not by Cambridge scientists James Watson and Francis Crick, but by the Swiss physician Friedrich Miescher who discovered a microscopic substance in the pus of discarded surgical bandages in 1869. In 1953, Watson and Crick proposed the double-helix model of DNA structure in the journal *Nature*. Their model was based on an unpublished X-ray diffraction image taken by Rosalind Franklin (in the photo) and Raymond Gosling in 1952. Watson and Crick (together with Wilkins, Franklin's supervisor) were jointly awarded the 1962 Nobel Prize in Physiology or Medicine. Despite her pioneering work, Rosalind Franklin was not included because, at that time, Nobel Prizes were awarded only to living recipients and she died of cancer in 1958 at the age of 37. The debate continues to this day about who should receive credit for the discovery. Many people have argued that Franklin should also have been awarded the Nobel Prize. (NF)

DNA and RNA

- Deoxyribonucleic acid (DNA) is a molecule that encodes the genetic instructions used in the development and functioning of all known living organisms. Most DNA molecules consist of two long polymer strands coiled around each other to form a double helix.
- The two DNA strands are composed of simpler units called nucleotides. Each nucleotide is composed of a nitrogen-containing base known as guanine (G), adenine (A), thymine (T), or cytosine (C) and a sugar called deoxyribose and a phosphate group. According to fixed rules for pairing the bases, A always goes with T and C with G.
- Like DNA, RNA (ribonucleic acid) is a chain of nucleotides, but unlike DNA it is more often found in nature as a single-strand. Furthermore, the nucleotide thymine is replaced by uracile (U) in RNA. Organisms use RNA to convert genetic information into specific proteins.
- Each of the three domains of life recognised by biologists today contain portions of DNA (e.g. rDNA, ribosomal DNA) which is unique to them, and this fact in itself forms the basis of the three-domain system and allows for the classification of organisms based on their DNA (phylogenetic approach).



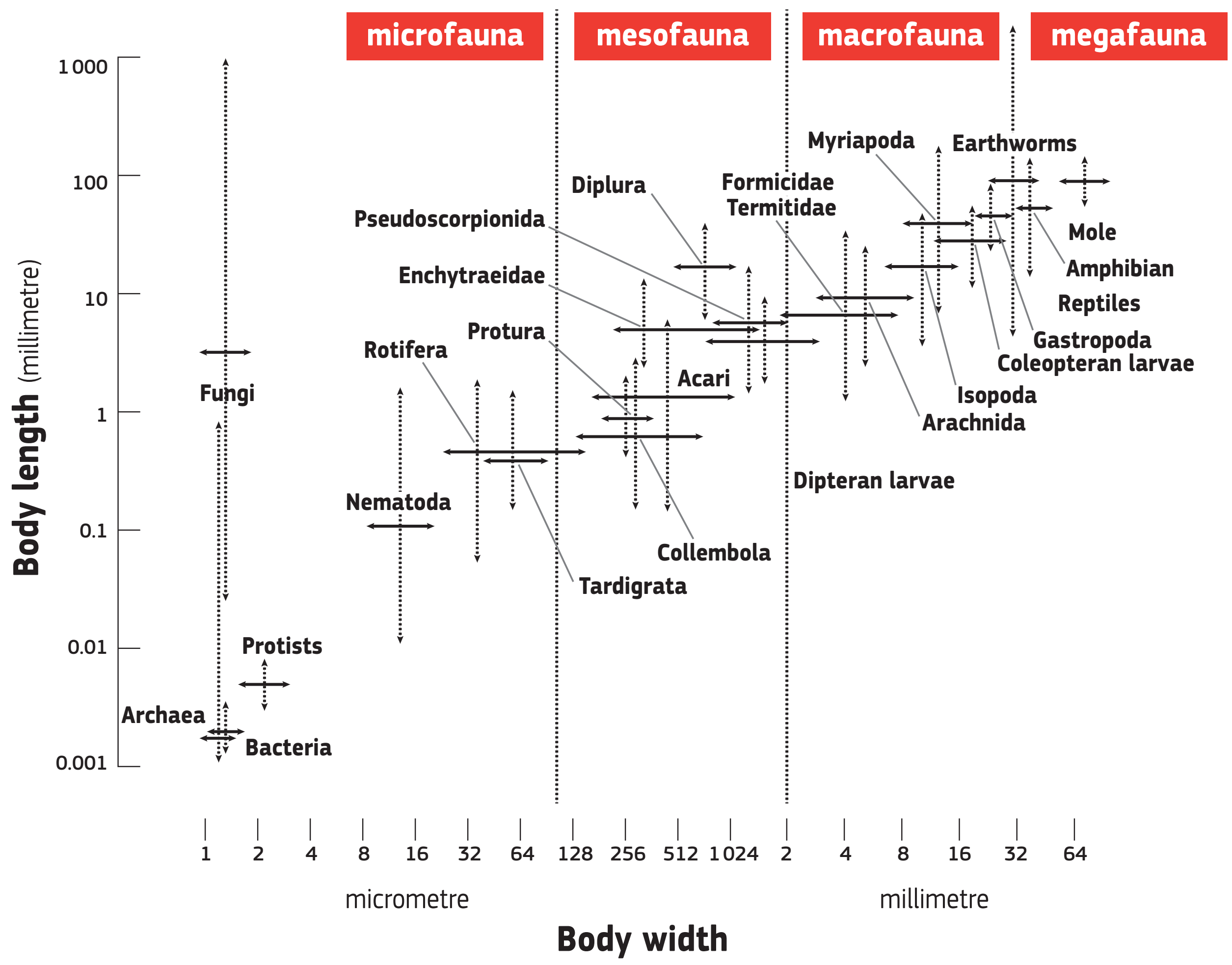
Structures of DNA and RNA. RNA presents a single strand, while DNA has the typical double strand helix. RNA and DNA are formed by four different nucleobases (nucleotides), three are present in both the molecules, namely cytosine, guanine and adenine. Thymine in DNA is replaced by uracil in RNA. (SP, RO)



Three-domain system of the biological classification of life on Earth showing the taxonomic groups described in this atlas (MJIB, LJ, JRC).

However, taxonomic classifications (i.e. using hierarchical ranks) provide little understanding of their lifestyles and functional roles. For this reason, this chapter explores the overwhelming diversity of soil biota using another common approach to classify soil organisms that involves using their body width to identify four broad groupings: microfauna (less than 0.1 mm), mesofauna (0.1 to 2 mm), macrofauna (2 to 20 mm) and megafauna (bigger than 20 mm). Body width appears to be a more consistent classifying criterion than body length, which shows greater variability even among representatives of the same group. However, even these ranges do not provide distinct limits and, on some occasions, there is some confusion as to whether a particular organism should be considered macro, meso or micro.

The size distribution of soil animals, together with some of their anatomical features (such as the presence/absence of legs) and some behavioural responses (reactions to light and heat), determine the best collecting method for a particular group of organisms. For example, the soft bodies of the microfauna and some of the mesofauna living in the water film surrounding soil particles can be extracted using a wet extraction method (Bearmann funnels; see pages 64-65) or by centrifugation. By contrast, the legged microarthropods with hard exoskeletons can be collected using dry extraction (Tullgren funnel; see pages 64-65) because these animals actively move away from light and heat. Finally, hand-sorting and pitfall trapping are often used to collect the macrofauna, while bait trapping has been used to catch mammals such as moles. All of these organisms are involved in creating and maintaining the soil structure and providing essential ecosystem services for humans (such as regulating greenhouse gas emissions or preserving water quality). Most of them cannot survive outside of soil, so it is necessary to preserve healthy and diverse soil systems if we want to preserve their beneficial influence. One of the main challenges that soil conservation faces today is the lack of awareness of the ecological importance of soil biodiversity. So, open your eyes and discover what lives under your feet!

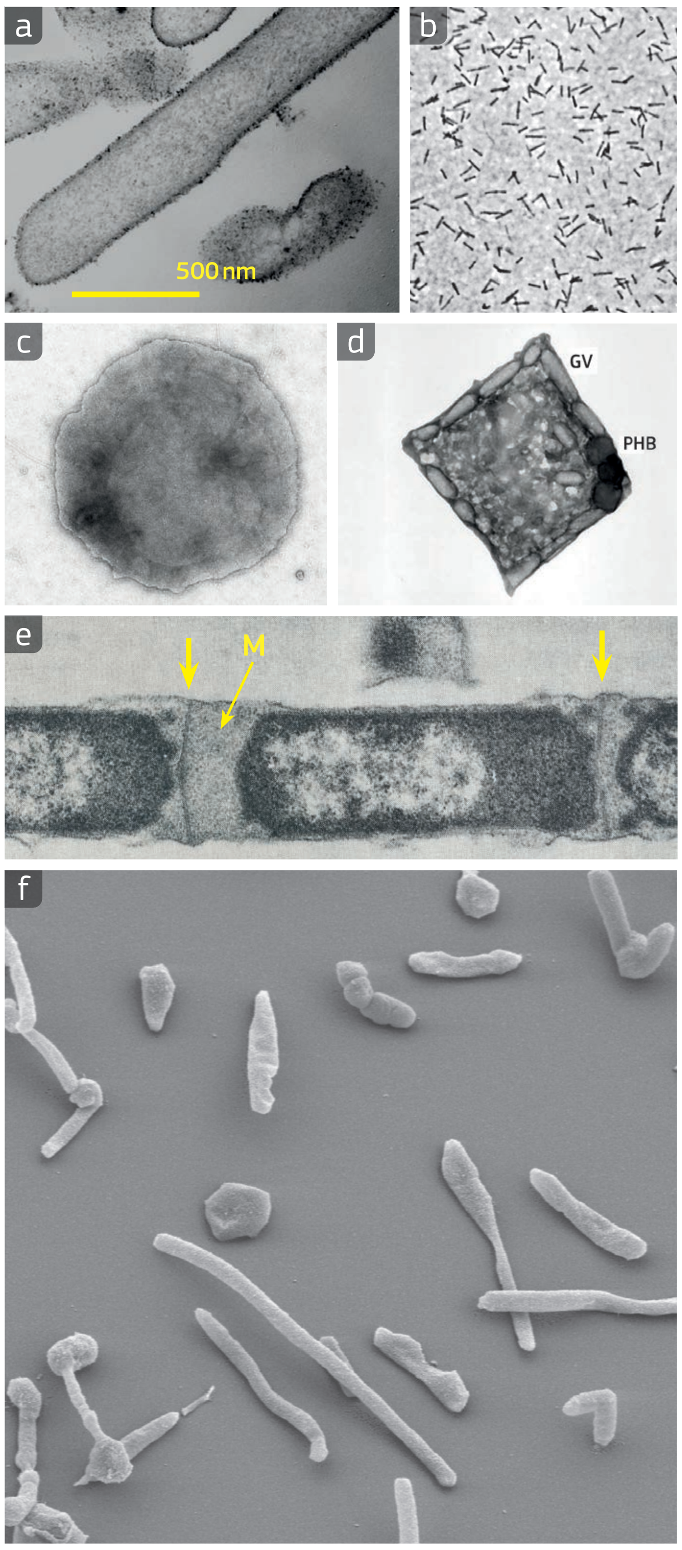


Body length and width of major groups of soil organisms. Size ranges are given for adult specimens and are approximate (derived from Swift *et al.*, 1979). (NK) [24]

Prokaryota – Archaea

Morphology

Archaea are unicellular microscopic organisms with a striking variety of cell shapes (pleomorphism) and unique geometric forms [25]. Many are rod-like (referred to as bacilli – e.g. *Methanocella* and *Methanobrevibacter*) or spherical (referred to as cocci – e.g. *Methanococcus*) while the heat-loving (thermophiles) *Sulfolobus* are highly irregular cocci. By contrast, *Methanosaeta* and *Methanospirillum* have both a long rod shape (filamentous) with sheaths that surround adjoining cells. Additionally, some archaea (e.g. *Methanosarcina*) form clusters, while the cells of *Haloterrigena* form many irregular shapes. Some species belonging to Halobacteriales can be square-shaped, triangles or flat discs.



Diversity of cellular shapes in the archaea: (**a**) Transmission electron microscopy (TEM) image and (**b**) phase contrast micrograph of rod-shaped *Methanocella conradii* cells; (**c**) TEM image of a coccoid *Methanococcus*; (**d**) Scanning electron microscopy (SEM) image of a square Halobacteriales cell with visible gas vesicles (GV); (**e**) TEM image of a *Methanosaeta* sheaf of cells, showing the spacer plug (arrowheads) and amorphous granular matrix (M); (**f**) SEM image of pleiomorphic *Haloterrigena turkmenica* cells. (ZL, DBN, DGB, TJB, ELS)

Diversity, abundance and biomass

Over 300 archaeal species have been described, primarily found in extreme environments. However, many more species have been detected in the environment but it is not possible to isolate and describe them. Soils contain between 10^5 and 10^{10} microbial cells in each gramme (0.04 ounces), and all contain archaea. Generally, up to 10 % of microbial cells in temperate soils may be archaea (mesophilic species), while in conditions of high temperature, high salinity or at high or low pH, archaea (extremophilic species) can be the dominant members of the microbial community.

Taxonomy

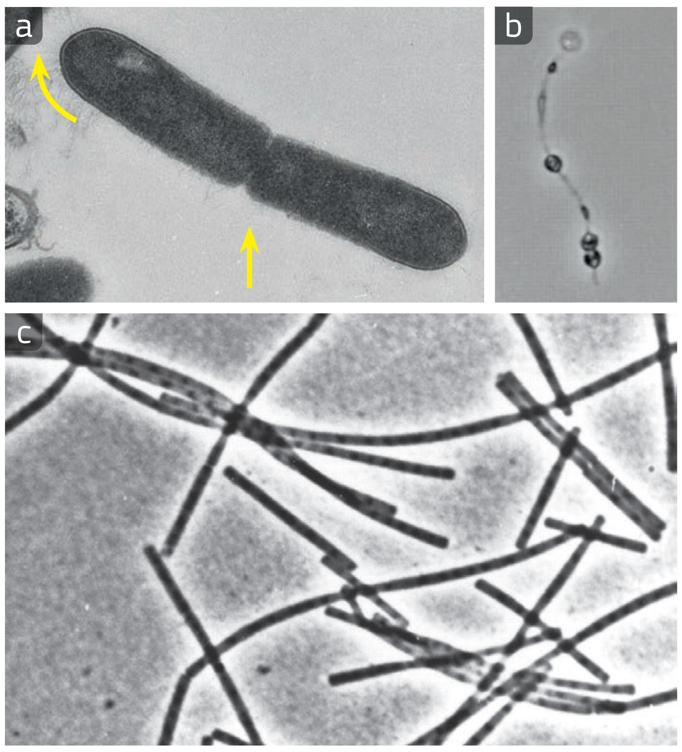
Archaea, the third domain of life (see page 31), were originally split into two phyla, the Euryarchaeota and the Crenarchaeota. The Crenarchaeota have now been divided to make a new phylum, the Thaumarchaeota. There may be other phyla, such as the Korarchaeota, Nanoarchaeota and Aigarchaeota, but whether these represent true distinct phyla is disputed. The Euryarchaeota are physiologically the most diverse, with a number of methane-producing orders (methanogens); the aerobic, salt-loving (halophilic) Halobacteriales; the thermophilic, Thermoplasmalates, sometimes lacking a cell wall; and several 'orders' with members that are not yet described. The Crenarchaeota are almost all extremophiles, living at high temperatures or extremes of pH (see boxes below) and are primarily involved in sulphur or iron metabolism. The Thaumarchaeota contain most of the isolated mesophilic archaea, which are associated with aerobic ammonia oxidation (nitrification). All three major phyla also contain many undescribed groups and we know little about their ecology and physiology.

Microorganisms and the environment

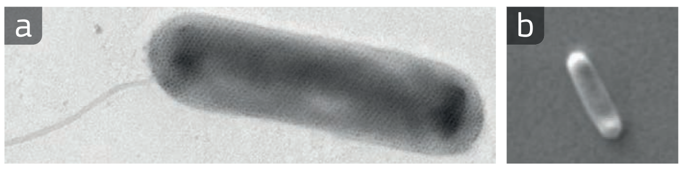
- Some microorganisms, including the archaea, are able to modify their shape or size in response to environmental conditions – this is also known as pleomorphism.
- Organisms that exist only in moderate temperatures, typically between 20°C and 45°C, are referred to as mesophiles.
- By contrast, extremophiles are organisms that thrive in extreme environmental conditions. It is possible to have different classes of extremophiles, depending on the evironmental factors:
  - thermophile: an organism that loves high temperature;
  - psychrophile: an organism that loves low temperature;
  - alkaliphile: an organism that loves high pH values;
  - acidophile: an organism that loves low pH values;
  - halophile: an organism that loves high salt concentration.

The versatile archaea

- The discovery of archaea altered our understanding of evolution, but recent research suggests that eukaryotes evolved from archaea. So humans may actually be derived from archaea.
- Archaea live in the widest range of environmental conditions of any organisms, from pH 0 to pH 12, 0˚C to 120˚C, and up to 35 % salinity.
- Hyperthermophilic archaea survive at temperatures greater than 90°C by having a thin membrane, made up of double-headed lipids, that insulates the cell interior from the heat. In acid or salty environments, this sort of membrane acts as a barrier to water molecules and other ions.
- The halophilic archaeon, now called *Haloquadratum walsbyi*, was for a long time known as 'Walsby's square bacterium' as it is box shaped and forms large fragile flat sheets in the environment.
- Archaea do not have a nucleus.



Euryarchaeota: (**a**) TEM image of a *Methanobrevibacter* from the gut of a soil insect; (**b**) Light micrograph of a Thermoplasmalates – its cells joined like beads on a string; (**c**) SEM image of *Methanosaeta* filaments. (JRL, TI, RG)



Thaumarchaeota: (**a**) SEM image of '*ca.* Nitrosotenuis uzonensis', a thermophilic ammonia oxidiser that is able to convert ammonia into nitrogen; (**b**) SEM image of *Nitrosotalea devanaterra*, an acidophilic that is also able to oxidise ammonia. (EVB, LEL)

Microhabitat

Euryarchaeota, in particular methanogens, dominate waterlogged soils. Six of the seven methanogen orders can be found in different soil types, either free-living or associated with other organisms, such as ciliates and termites. Methanogens can also be found in dry and aerated soils. Members of the Halobacteriales order are often found in high salinity soils, and many use light as an energy source. Archaea in soils under termperate climates are dominated by the Thaumarchaeota, a group that was previously linked to the Crenarchaeota. Many Thaumarchaeota are able to convert ammonia to nitrite (amonia-oxidisers). In low pH soils, and under low ammonia and low oxygen conditions, these archaea are more important than their bacterial counterparts. There are also non-ammonia oxidising Thaumarchaea, but it is not possible to isolate these in the laboratory (see pages 64-65); therefore, they remain uncharacterised. The extremophilic Crenarchaeota are primarily found in harsh soils, such as hot volcanic soils, rich in sulphur and iron compounds. A unique group was found to be the dominant archaea in high acidic, deeply weathered, red soils (Ferralsols – see pages 26-27) in China.

An extremely hot, sulphur-rich environment (Campi Flegrei, Italy). Thermophilic Archaea of the phylum Crenarchaeota can be found in the soils around volcanic vents (fumaroles). (YIF)

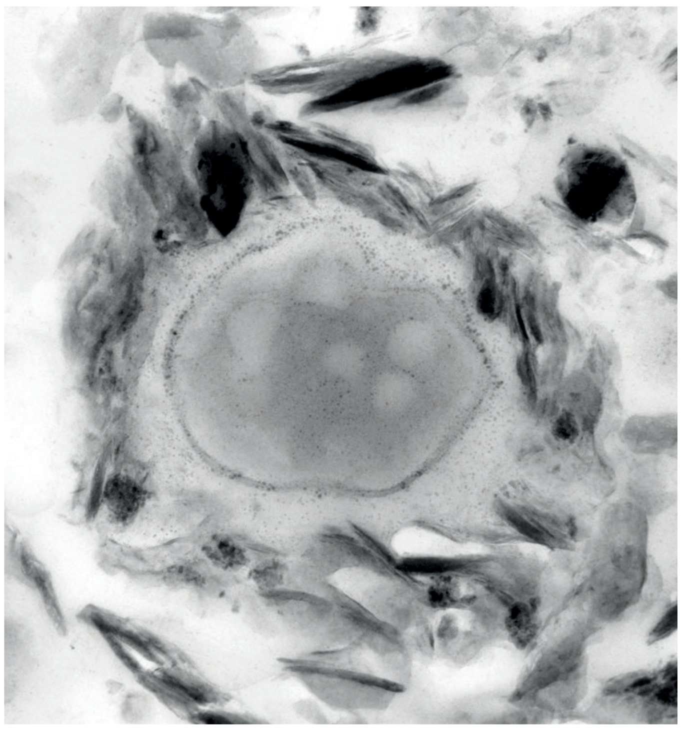
Prokaryota – Bacteria

Morphology

Bacteria are one of the two domains, along with Archaea, that include prokaryotic organisms [26]. The domain Bacteria comprises microscopic organisms, single-celled or with the cells forming simple associations. Most bacteria are 0.2 micrometres (μm) in diameter and 2-8 μm in length. Bacteria have a variety of shapes: round or spherical (commonly known as cocci), rod shaped (bacilli) and spiral (spirilla). However, many bacteria can assume several shapes (pleomorphic). Depending on how the newly formed cells adhere to each other, bacterial arrangements include singles, pairs, chains and clusters. When bacteria are motile (capable of moving) they have a specific structure (flagellum) for locomotion. The flagellum is a whip-like structure that can occur at one end, both ends, or all over the bacterial cell. Bacteria can live without oxygen (anaerobes) or depend on it to grow (aerobes). They can also be adapted to live either in the presence or absence of oxygen (facultative anaerobes). Some species of bacteria contain endospores or exospores (see box next page). If you break down the term endospore, 'endo-' means 'inside' and '-spore' refers to the 'dormant structure', so the endospore is a structure of resistance formed inside the cell. By contrast, the exospores develop externally. Spores are a bacterial cell's way of protecting itself against harsh changes in the environment or nutrient depletion. A spore protects the bacterial genetic material so that, when optimal conditions return, the bacterial cell can reform (germinate) and thrive again.

Taxonomy

Currently, there are 30 known and recognised phyla of bacteria. Highly diverse and abundant phyla in soil are Proteobacteria, Firmicutes, Actinobacteria and Cyanobacteria (see pages 34-35). However, some other phyla, such as Acidobacteria, can also be found in soil.



Transmission electron micrograph showing a soil bacterium (circle in the middle) surrounded by clay particles and compounds (polysaccharides) released by the bacterium itself. (CC)

Bacterial phyla

- In contrast to eukaryotic nomenclature, there is no official classification of prokaryotes because taxonomy remains a matter of scientific judgment and general agreement.
- The List of Prokaryotic names with Standing in Nomenclature (LPSN) is an online database that maintains and provides accurate names (nomenclature) and related information of prokaryotes according to the International Code of Nomenclature of Bacteria.
- The 30 phyla currently accepted by the LPSN are: Acidobacteria; Actinobacteria; Aquificae; Armatimonadetes; Bacteroidetes; Caldiserica; Chlamydiae; Chlorobi; Chloroflexi; Chrysiogenetes; Cyanobacteria; Deferribacteres; Deinococcus-Thermus; Dictyoglomi; Elusimicrobia; Fibrobacteres; Firmicutes; Fusobacteria; Gemmatimonadetes; Lentisphaerae; Nitrospira; Planctomycetes; Proteobacteria; Spirochaetes; Synergistetes; Tenericutes; Thermodesulfobacteria; Thermomicrobia; Thermotogae.
- Other existing phyla of bacteria, which cannot currently be cultured in the laboratory (see pages 64-65), are called candidate phyla. If these are included, the total number of phyla is 52.

Typical structures, the nodules, occur on the roots of plants that associate with symbiotic nitrogen-fixing bacteria. Nodules in the roots of (**a**) *Mimosa foliolosa*, a plant native to Brazil, formed by the nitrogen-fixing bacteria *Burkholderia* sp., (**b**) cowpea (*Vigna unguiculata*) formed by *Bradyrhizobium* sp. and (**c**) *Medicago italica* formed by *Sinorhizobium meliloti*.(FC, FMSM, NI)

Diversity, abundance and biomass

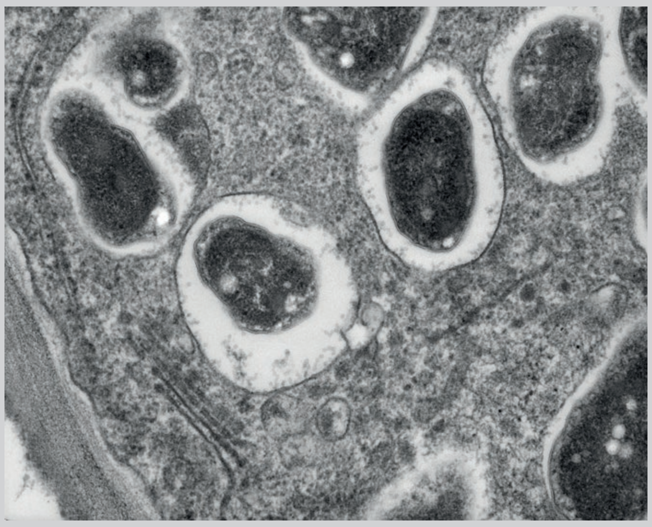
Most microbial species (more than 90 % according to the current estimates), including bacteria, still remain unculturable (i.e. they cannot be grown in any culture medium in the laboratory). This means that we do not yet know what they look like or what functions they carry out. Advances in molecular techniques (see pages 64-65) in the past 30 years have enabled us to understand more about these species by sequencing parts of their DNA. These advances have also allowed for the identification of new culturable species. Today there are approximately 2 800 genera comprising approximately 15 000 species of known bacteria. Soil microbial biomass is made up of bacteria, fungi and other microorganisms. This biomass represents 1 to 4 % of total soil carbon (up to three tonnes of carbon per hectare). The ratio of the size of bacterial to fungal biomass depends on soil properties and other environmental factors (e.g. soil pH, temperature and nutrient availability); for example, a 30-fold decrease in bacterial biomass was found when comparing high to low pH soils.

Microhabitats

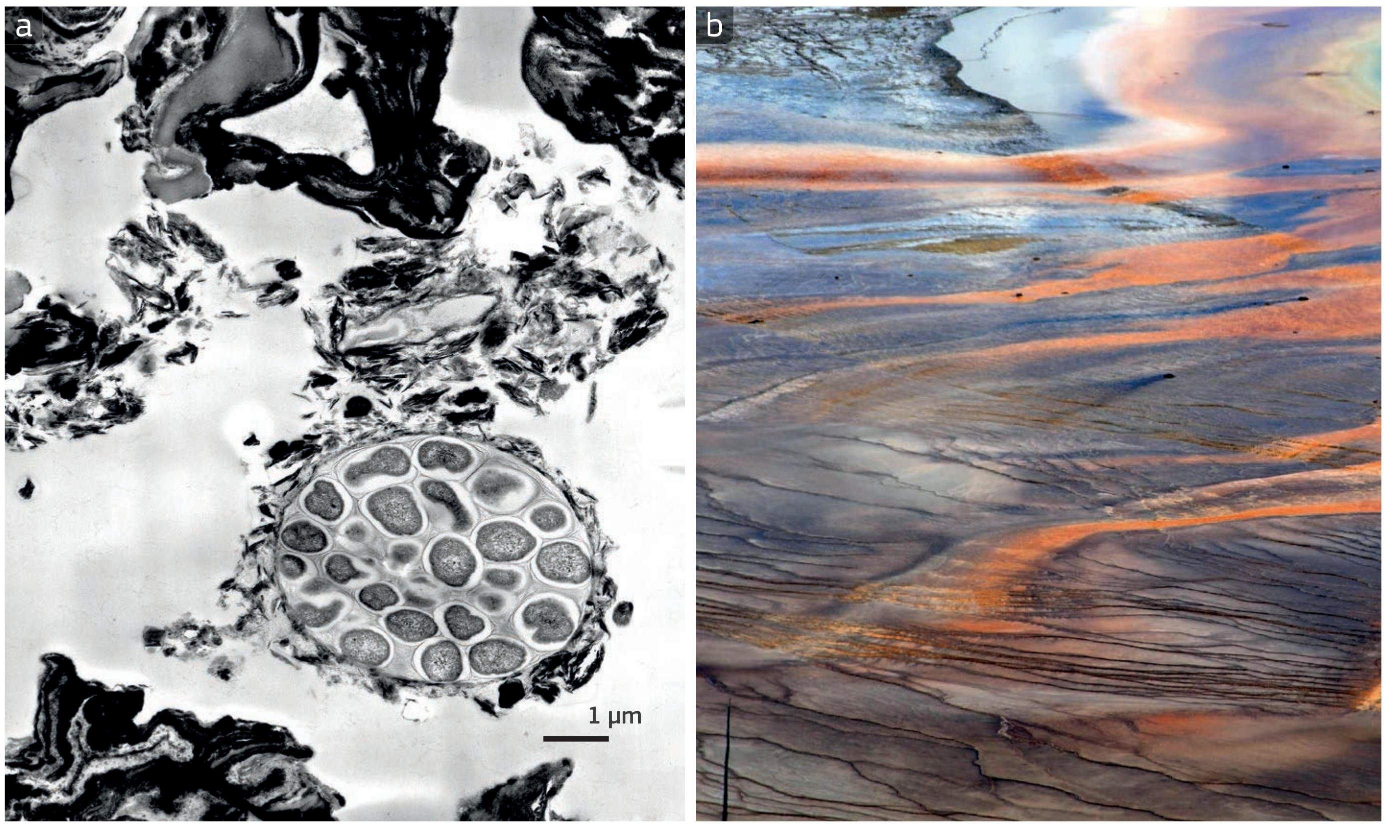
Unlike eukaryotes, bacteria can be found in a wide range of environmental, chemical and physical conditions including extremes of pH, temperature and salinity. Many soil bacteria are beneficial to human economic activities and are necessary for environmental sustainability. Bacteria are part of chemical cycles during which they release essential elements for recycling. They also decompose dead organic matter and are the only microbes capable of biological nitrogen N_2 fixation (see page 105). This is the ability to transform nitrogen (N_2) from the atmosphere (about 80 % of the atmosphere is N_2) into ammonium (NH_4^+) which is assimilated by eukaryotes, plants in particular. Bacteria can exist either as independent (free-living) organisms or as symbionts that depend on other organisms to live, subsisting either as mutualists, parasites or commensalists (see box below).

What is symbiosis?

- Symbiosis is a close and often long-term interaction between two different biological species.
- There are three main types of symbiosis:
  - mutualism is the way two organisms of different species exist in a relationship in which each individual benefits from the activity of the other;
  - commensalism is a class of relationship between two organisms where one organism benefits from the other without affecting it;
  - parasitism is a relationship between species, where one species, the parasite, benefits at the expense of the other, the host.
- Some symbiotic relationships are obligate, meaning that both symbionts entirely depend on each other for survival.
- Other relationships are facultative, meaning that they are not essential for the survival of either species. Individuals of each species engage in symbiosis when the other species is present.



The soil bacterium *Bradyrhizobium japonicum* colonises the roots of some plants and establishes a symbiosis. This high magnification image shows part of a plant cell with bacterial cells (dark circles) in it. (LH/DEMF)



(**a**) Soil bacteria living within the soil particles. They can also be found in extreme environments: (**b**) the reddish and brownish colours are mats of bacteria living around geothermal hot springs in Yellowstone Park in the USA. (FW, FKO)

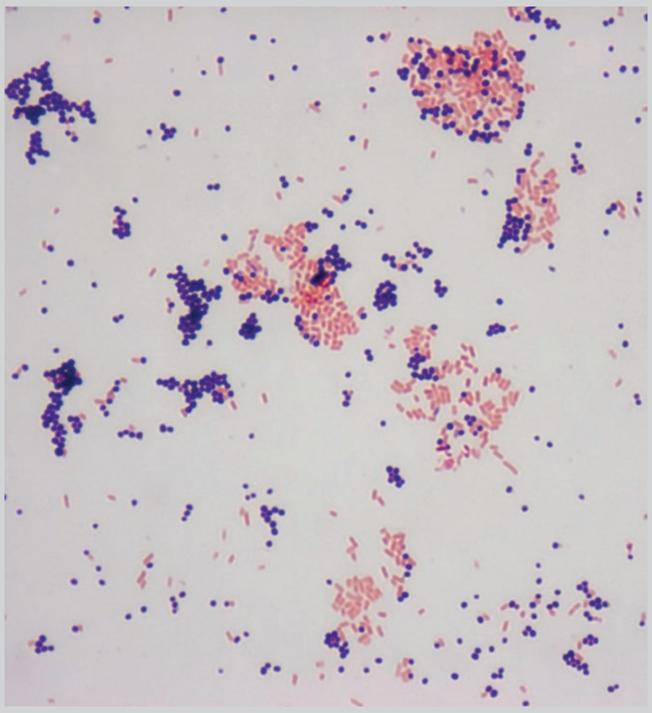
Prokaryota – Bacteria

Proteobacteria

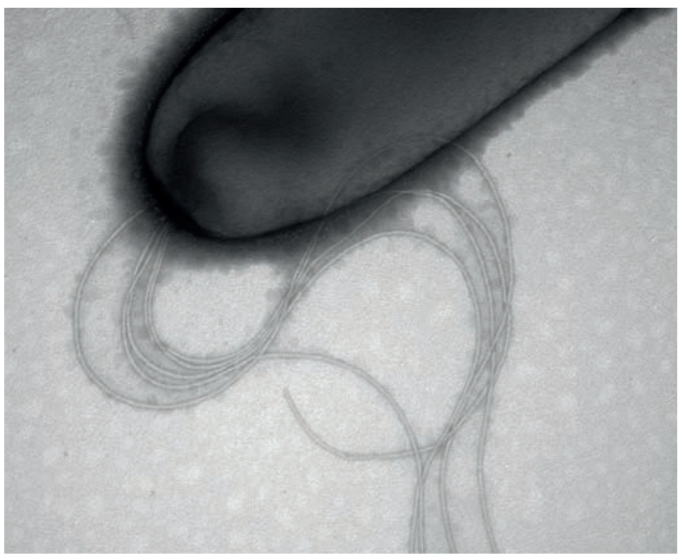
Proteobacteria is the largest and most diverse bacterial phylum [26]. It contains about 30 % of the total number of bacterial species. Proteobacteria comes from the name of the Greek god *Proteus*, which could take various forms, thus reflecting the enormous diversity of morphological and physiological characteristics observed in this bacterial phylum. Proteobacteria comprises the majority of Gram-negative (see box below) bacteria of medical (e.g. *Helicobacter*), veterinary (e.g. *Acinetobacter*), industrial (e.g. *Campylobacter*) and agricultural interest (e.g. *Bradyrhizobium*). It also comprises bacteria involved in carbon, sulphur and nitrogen cycles (including N_2 fixers – see pages 99, 105), phototrophic (i.e. organisms that obtain energy from light) and non-phototrophic, aerobic and anaerobic bacteria.

Gram-positive and Gram-negative

- Gram staining, also called Gram's method, is a method of differentiating bacterial species into two large groups: Gram-positive and Gram-negative, respectively. The name comes from the Danish bacteriologist Hans Christian Gram, who developed the technique. The technique is based on the use of a chemical compound, the crystal violet. The name refers to its colour, similar to that of the petals of a gentian flower. The Gram stain is almost always the first step in the identification of bacterial organisms.
- Gram-positive bacteria are bacteria that give a positive result in the Gram stain test. Gram-positive bacteria take up the crystal violet stain used in the test, and then appear to be purple-coloured when seen through a microscope. This is because in the cell wall of the Gram-positive bacteria there is a layer that retains the stain after it is washed away from the rest of the sample, in the decolourisation stage of the test.
- Gram-negative bacteria are a group of bacteria that do not retain the crystal violet stain. After staining with crystal violet, the excess is washed off with alcohol, which decolourises the bacteria since the layer in their cell wall is too thin to retain the stain. A counterstain is then added, which colours the bacteria red or pink.



Two species of bacteria, one of which is a Gram-positive coccus (*Staphylococcus aureus*, stained dark purple) and the other a Gram-negative bacillus (*Escherichia coli*, stained pink). (MP)



Transmission electron microscope image of *Pseudomonas aeruginosa*. *Pseudomonas* is a genus of Gram-negative Proteobacteria that can be found in many different environments, including soil. (LH/DEMF)

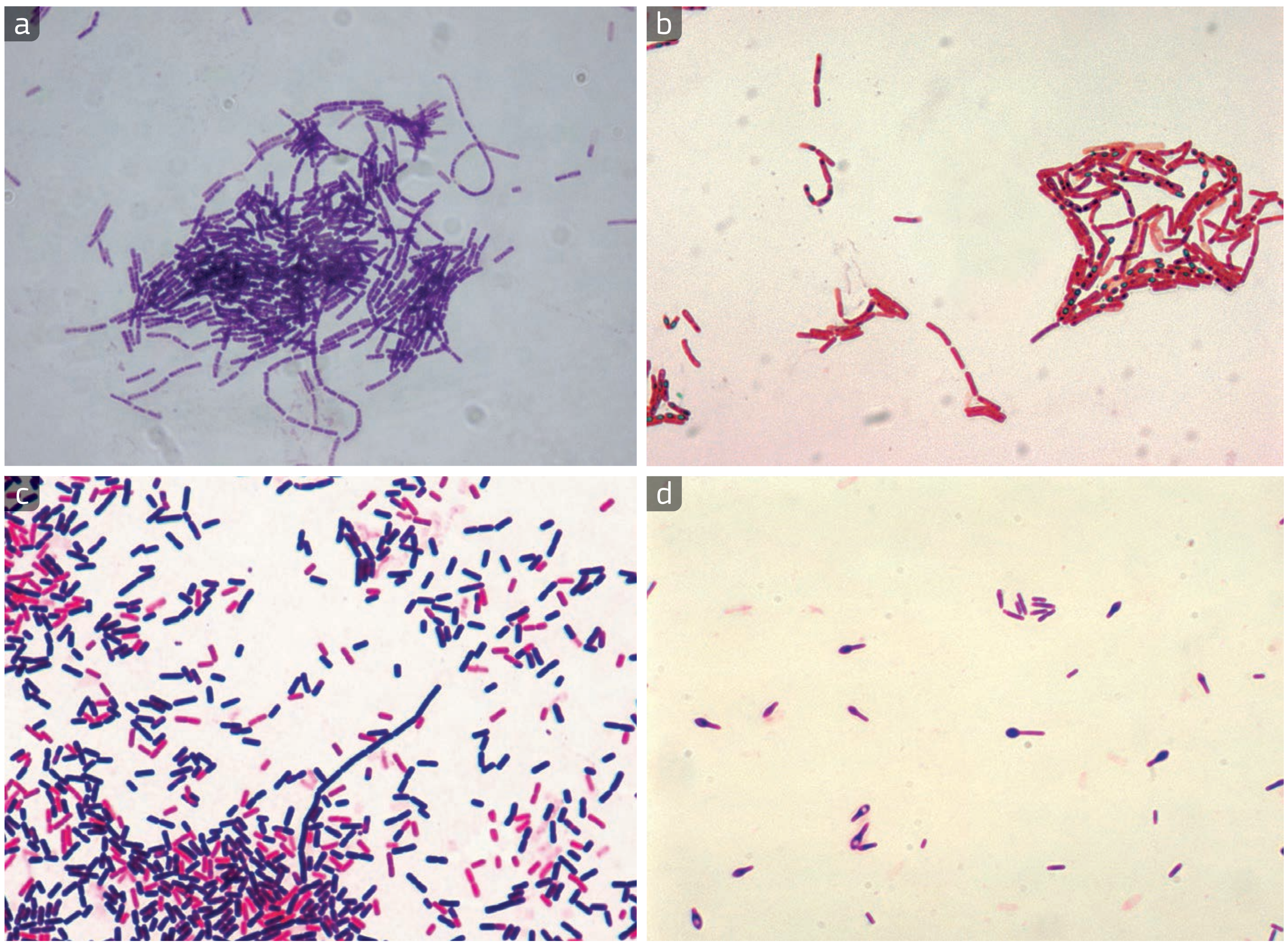
Firmicutes

The most representative genera in Firmicutes are *Bacillus* and *Clostridium,* which are obligate and facultative anaerobic bacteria, respectively [26]. These genera include important species of human and animal pathogens that produce resistant cell structures called endospores. Spores tolerate different types of stresses. For example, they are more resistant to heat than normal cells by a factor greater or equal to 10^5. Furthermore, they are 100 times or more resistant to ultraviolet radiation, and more tolerant to drought, antibiotics and disinfectants. Most *Bacillus* species, such as *B. cereus*, which causes contamination of food, are soil inhabitants. Due to their pathogenicity on some soil insects, some *Bacillus* species, including *B. popilliae*, *B. lentimorbus* and *B. thuringiensis*, have been successfully used in agriculture to control pests. *Bacillus* may also be dangerous: *Bacillus anthracis* is considered the most lethal biological weapon for human beings because it is the origin of anthrax (see box on page 108). Another Firmicute genus, *Paenibacillus,* includes important soil-living nitrogen fixers (see page 99). Nitrogen-fixing bacteria are also present in both *Bacillus* and *Clostridium* genera.

Bacteria as workers

- Many compounds are produced in large amounts by bacteria to be used for various purposes in industry and medicine. They can be a part of silk, cotton and rubber manufacturing. Bacteria also synthesise certain antibiotics, such as bacitracin and polymyxin.
- Bacteria are able to degrade complex compounds. For example, they break down the woody and tough tissues of jute, coconut, hemp and flax. They can also degrade hydrocarbons and clean up oil spills.

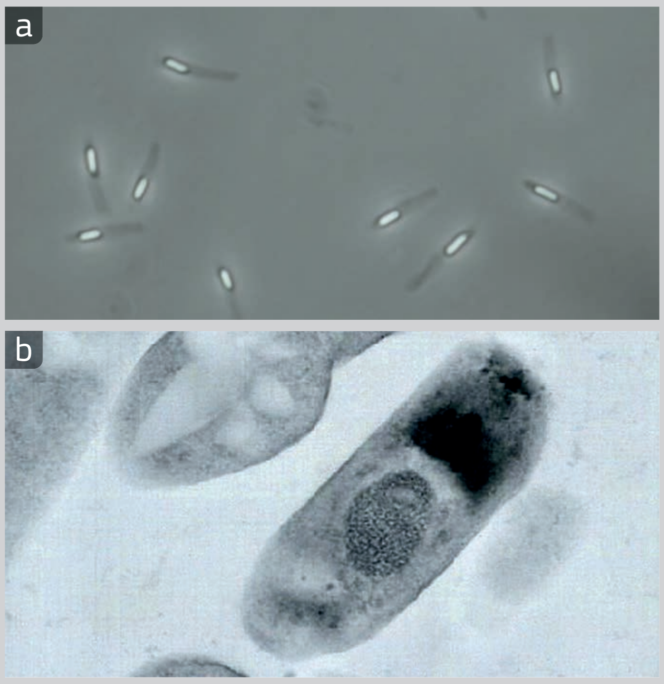
Bacteria can be used to 'eat' oil spills. (LSU)



(**a–b**) *Bacillus* and (**c–d**) *Clostridium* are the two most important genera of the phylum Firmicutes. *Bacillus* species are able to colonise a variety of habitats ranging from soil and insects to humans. *Clostridium* species from soil samples, manure and plant materials can be easliy grown and studied. (DS, LS, UCSFMC, GL)

Endospores, what are they?

- Endospores can survive environmental assaults that would normally kill the bacterium. These stresses include high temperatures, high UV irradiation, desiccation and chemical damages. The extraordinary resistance properties of endospores make them of particular importance because they are not readily killed by many antimicrobial treatments.
- When favoured nutrients are exhausted, some Gram-positive bacteria may develop an extreme survival strategy: the formation of endospores.
- This complex development allows the bacterium to produce a highly resistant cell to preserve the cell's genetic material in times of extreme stress.
- The resilience of an endospore can be explained in part by its unique cellular structure. The outer coat surrounding the spore provides much of the chemical resistance. Beneath the coat there is a very thick layer called the cortex. Proper cortex formation is needed for dehydration of the spore core, which aids in resistance to high temperature. A germ cell wall is found under the cortex. This layer will become the cell wall of the bacterium after the endospore germinates. The inner membrane, under the germ cell wall, is a major permeability barrier against several potentially damaging chemicals. The centre of the endospore, the core, exists in a very dehydrated state and houses the cell's DNA.
- The process of forming an endospore is complex and requires several hours to complete.



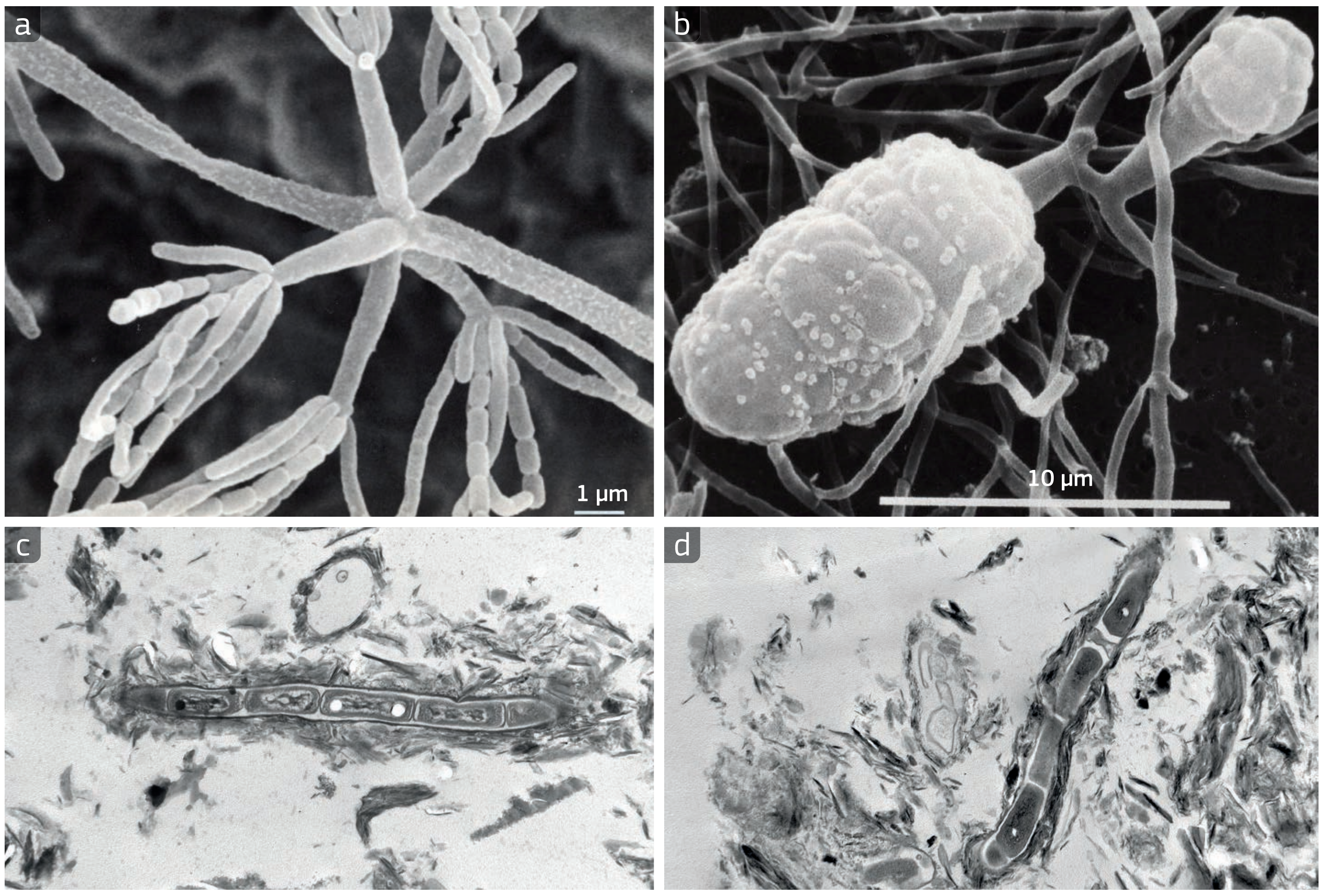
Endospores of the Firmicutes (**a**) *Paenibacillus alvei* and (**b**) *Bacillus anthracis* are clearly visible (white spots and dark circle, respectively) inside bacterial cells. (TE, SZ)

Actinobacteria

Actinobacteria is a phylum of Gram-positive bacteria that have a highly diverse morphology, ranging from micrococci (spherical) and rods to branched filaments that resemble fungal hyphae (see box on page 39) [26]. The bacterial filaments are narrow (diameter from 0.5 to 2 µm) and can be short and rudimentary or extensively branched. Throughout their life cycles, Actinobacteria may combine these different forms. Their reproduction is by fragmentation of hyphae or through the production of spores. The spores may be of several types (e.g. arthrospores, very primitive spore type, formed through the breaking up of hyphal filaments in *Streptomyces* and zoospores, motile and flagellate spores, in *Spirillospora* and *Actinoplanes*). Spores are produced (from one to several in chains) on hyphae, in spore-producing structures (sporangia) or vesicles. The ecological niche of most Actinobacteria is the aerobic zone in soil. A striking feature of Actinobacteria is the production of extracellular enzymes that degrade complex macromolecules commonly found in soils (e.g. casein, starch, chitin, cellulose and lignocellulose). Furthermore, they synthesise and excrete thousands of metabolites, such as antibiotics. For example, Selman Waksman, one of the most important soil microbiologists, won the Nobel Prize for Medicine in 1952 for his discovery of streptomycin produced by bacteria of the genus *Streptomyces*. In addition to streptomycin, Streptomyces are capable of producing a wide variety of antibiotics with numerous properties: antibacterial, antifungal, antiviral, antitumor, antiparasitic, insecticide and weed controlling. Actinobacteria also includes the nitrogen-fixing bacteria of the genus *Frankia*, which form root symbioses with plants of eight botanical families (e.g. Betulaceae – see page 43). Other species belonging to the genera *Streptomyces* and *Corynebacterium* are plant pathogens. Animal pathogens are found among the genera *Corynebacterium*, *Actinomyces*, *Nocardia*, *Thermoactinomyces* and *Mycobacterium*. Among them, the *Mycobacterium avium-intracellulare-scrofulaceum* stands out as being lethal for people who have contracted the human immunodeficiency virus (HIV).

Why does the air smell of soil after rain?

- The earthy smell after it rains is linked to Actinobacteria.
- In particular, the molecule responsible for the aroma is known as geosmin.
- Geosmin is produced by the Gram-positive bacterium *Streptomyces*, a genus of Actinobacteria, and released when these microorganisms die.
- The human nose is extremely sensitive to geosmin and is able to detect it at very low concentrations.
- Geosmin is also responsible for the earthy taste of beetroots.

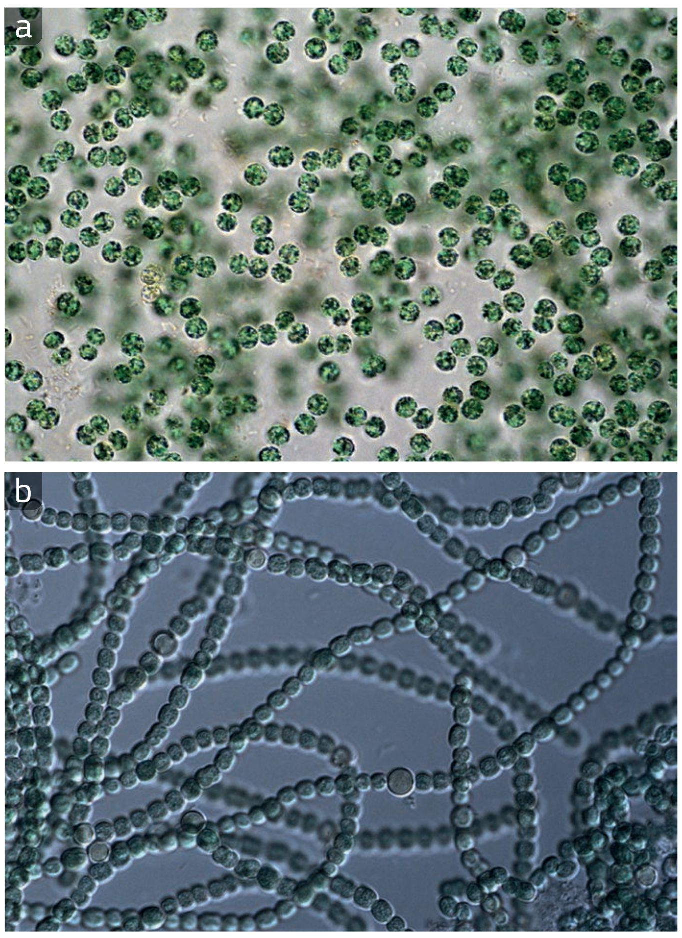


Scanning electron images show (**a**) branching filaments (hyphae) of *Streptomyces verticillus* with spores at their ends and (**b**) two young spore-producing structures (sporangia) developed from a single hypha of a *Frankia* species. (**c**-**d**) Actinobacteria among soil particles. (TH/MHA/SAJ, DDB/HAL/SAJ, FW)

Different species of Actinobacteria can be identified by growing them on artificial substrates made with jelly-like substances and nutrients such as oatmeal (see pages 64-65). Different colours and shapes allow the distinction of different species. (PT/FIIRV)

Cyanobacteria

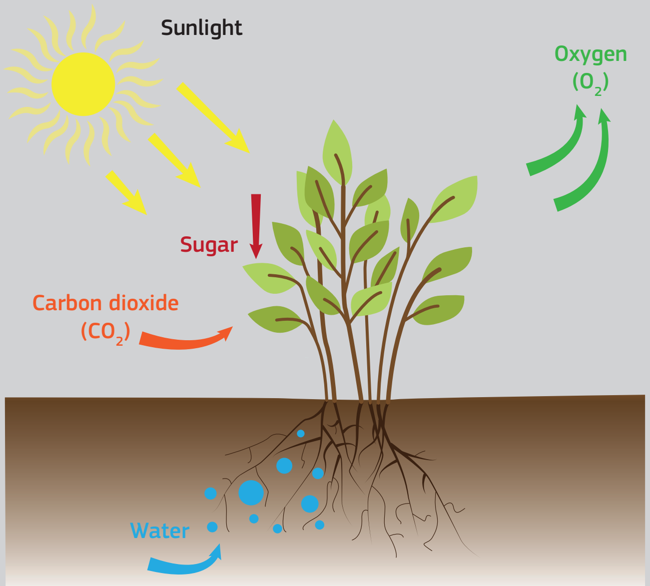
Cyanobacteria is a group of bacteria that are able to obtain their energy through photosynthesis. This is possible due to the presence of chlorophyll, which is also found in other photosynthetic organisms, such as algae and plants. Being photosynthetic, they manufacture their own food. This has caused them to be dubbed 'blue-green algae', though they have no relationship to any of the various eukaryotic algae. They are considered one of the most diverse groups of prokaryotes as they vary from unicellular to complex filamentous or branched forms. In some cases they have highly differentiated cells that carry out different functions, so they may be considered as truly multicellular organisms. Cyanobacteria have the distinction of being the oldest known fossils, more than 3.5 thousand million years old, in fact. The cyanobacteria have been tremendously important in shaping the course of evolution and ecological change throughout Earth's history. Indeed, the atmospheric oxygen that we depend on was generated by numerous cyanobacteria through photosynthesis. Furthermore, the photosynthetic structure of plant cells, the chloroplast, evolved from cyanobacterial ancestors. Cyanobacteria also contribute to the health and growth of many plants in another way: they have the ability to convert inert atmospheric nitrogen into ammonia (nitrogen fixation) that plants can use (see page 105). This process cannot occur in the presence of oxygen, so nitrogen is fixed in specialised cells called heterocysts. These cells have an especially thickened wall that contains an anaerobic environment. Cyanobacteria also form symbiotic relationships with many fungi, forming complex symbiotic organisms known as lichens (see page 42).



Cyanobacteria can have different forms: (**a**) unicellular and (**b**) filamentous. In the filaments it is possible to see bigger cells, called heterocysts, where nitrogen fixation takes place. (KSI)

What is photosynthesis?

- Photosynthesis is a process used by plants, algae and cyanobacteria to convert sunlight energy into chemical energy.
- This chemical energy is stored in carbohydrate molecules, such as sugars, which are produced from carbon dioxide and water;
- Oxygen is released as a waste product.
- Photosynthesis maintains atmospheric oxygen levels and supplies most of the energy necessary for life on Earth.



Schematic of photosynthesis. The sugars produced are stored in or used by plants, whereas oxygen is released into the atmosphere. (JRC)

Protists

Protists are defined as unicellular eukaryotes (see page 30). Many form filaments (such as some fungi), are colonial or aggregate into larger clusters of cells. They are divided into the Archaeplastida (green algae, red algae and ancestors of higher plants), the Amoebozoa (many amoeboid species), the Opisthokonta (collar cells, fungi and ancestors of animals), Stramenopiles, Alveolata, Rhizaria and Excavata. Typically, they have one nucleus and soil species have a contractile vacuole for regulating water and ion concentrations. Many species have a swimming dispersal stage with one or more cilia. Cysts form in sub-optimum living conditions or when prey are scarce. Although many protists can be identified under the microscope to family or genus level, species identification is made through DNA sequence analysis (see pages 64-65). [27]

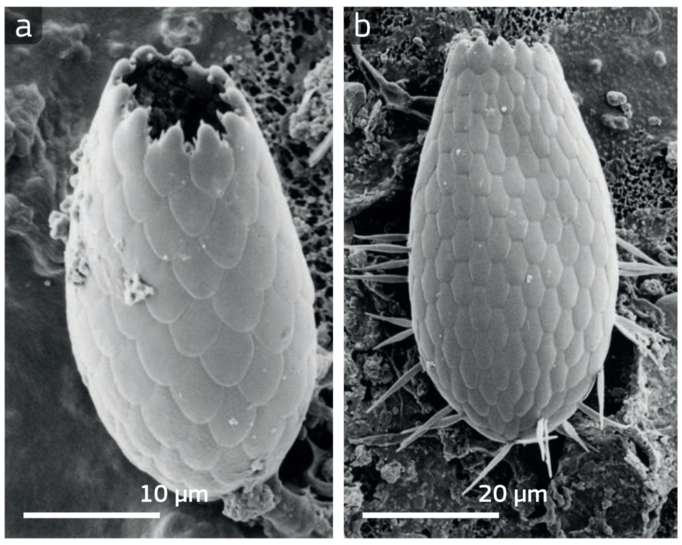
Rhizaria

Morphology

Cells typically produce very thin hair-like extensions called filopodia that can branch and merge together again, forming a complex network in some species. They tend to grow flat on surfaces and their filopodia can extend into small crevices in the soil searching for bacteria. When detached from surfaces, they swim with two cilia. They can also move by amoeboid locomotion or gliding on surfaces. Soil species form resting cysts that enable them to survive adverse environmental conditions. There are many variations of this basic morphology as it is a diverse group.

Taxonomy

This supergroup has one major soil lineage: the Cercozoa [28]. The Cercozoa (common name cercomonads) consist of a diverse variety of species of small bacterial-feeding unicells less than 10 µm in size. One subgroup common in soils is the Silicofilosea that secrete silica scales on their surface. The Silicofilosea also include the Euglyphida that form vase-shaped protective layers (known as tests) outside the cell. Other Cercozoa include Vampyrellida that feed on fungal hyphae (see box on page 39), the Phytomyxea that are parasites of plants and Stramenopiles (see page 37) and Ascetospora that are parasites on soil invertebrates.



The filose testate amoebas (**a**) *Euglypha rotunda* and (**b**) *Euglypha compressa* are Rhizaria species abundant in soil. (YE, SS)

Microhabitat

Rhizaria live on the surfaces of soil and organic matter particles where they select bacteria to ingest. Species may have depth preferences in the soil. Some prefer organic matter and litter on the surface of the forest floor. Others, such as Vampyrellida, prefer to penetrate fungal hyphae or spores. Those species with cilia can explore their habitat by swimming. The filopodia can extend into very small crevices (< 1 µm) to search for bacterial prey.

Diversity, abundance and biomass

There are hundreds or even thousands of soil Cercozoa species that cannot be distinguished by microscopy and, therefore, many genera remain to be described. These are usually the most common active protists in soils, and abundances vary with moisture as well as with the abundance of bacteria or other prey. Densities may reach more than one million cells per gramme of soil but are usually 10^3 - 10^5 per gramme.

Amoebozoa

Morphology

The Amoebozoa is another group of unicellular organisms whose cells are covered by a very thin protein layer with or without microscales. [29, 30]

Taxonomy

The Amoebozoa is a supergroup that contains bacterial-feeding amoeboid species. Several lineages contain mostly aggregative species referred to as 'social amoebae', such as the Myxogastria and the Dictyostelia, but aggregative species occur in other protists as well. In Arcellinida the cell is inside a vase- or helmet-shaped structure made of protein, sometimes amended with soil particles bound together by proteins.

Social amoebae

- Social amoebae occur among protists and not just in Amoebozoa.
- They are found in a wide variety of colours; more than 900 species of slime mould occur all over the world.
- Some species may reach sizes of several square metres and masses of up to 30 grammes.
- They live in any type of dead plant material and contribute to the decomposition process.

Fuligo septica is commonly known as the dog vomit slime mould or scrambled egg slime because of its peculiar yellowish colour. It grows on decaying wood but can also grow on plant leaves. (SI)

Microhabitat

Amoeboid species occur on moist surfaces and live in water microfilms where they forage for palatable bacteria or other prey. Some species prefer wet conditions, others occur in drier conditions, some have depth and litter preferences, and some are known colonisers and occur in disturbed soils where other species are absent. Amoeba are very effective at scouring surfaces for bacteria. A small number feed on fungal hyphae or prey on protists or microinvertebrates.

An Ameabozoa specimen from the Vannellidae family. Flattened, fan-shaped amoebae of this family were recognised as an important major amoebozoan taxon only in 2004. (YE)

Diversity, abundance and biomass

Although most genera have probably been described, and about 3 000 species have been identified, many species still remain to be discovered. When active, there can be as many as 100 000 cells per gramme of soil, but more typically numbers are 10^3 - 10^4, depending on the ecosystem.

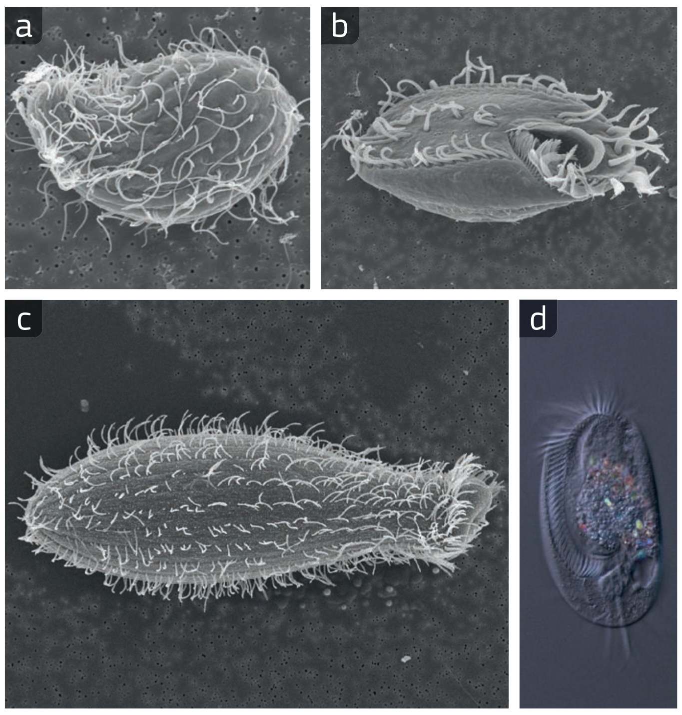
Alveolata

Morphology

The Alveolata is a group of protists characterised by folded membranes underneath their cell membranes (called alveoli) [31]. Ciliophora (the only soil-inhabiting Alveolata) have two types of nuclei: a small inactive nucleus with condensed chromosomes, which becomes active only during reproduction, and a large nucleus that is always active and holds many copies of the chromosomes. Most species have rows of cilia that beat in a coordinated manner, and a specialised funnel structure for capturing and ingesting prey. They also often have specific defensive or aggressive structures, called ejectosomes. These are made of mucus that is ejected from the cell. A complex network of vacuoles inside the cell regulates the digestion of food and the water balance.

Taxonomy

There are three main supergroups in the Alveolata (Apicomplexa, Dinoflagellata and Ciliophora), but only Ciliophora (ciliates) are found free-living in the soil. Most ciliates ingest bacteria, but some ingest other protists or are specialised symbionts or parasites (see box on page 33). Colpodellida prey on other protists and can reach higher numbers by feeding on soil invertebrate corpses. The Colpodea includes most of the ciliates found in high abundance when soil samples are kept in the laboratory. Many genera emerge from cysts when sufficient moisture and bacteria are present and then reproduce. Colpodids are very diverse and can be identified to the genus or family level (see page 29) through microscopy. The other genera that occur in some abundance in soils belong to the order Hypotrichea. These are also diverse but rarely dominant in terms of abundance. The Colpodid to Hypotrich ratio (also called the Colpodid to Stichotrich ratio) is used as an indicator of environmental quality.



Examples of Alveolata: (**a**) *Colpoda steinii* shows a shape that resembles a kidney; (**b**) *Steinia* sp. with a pointed tail (left side), typical of this genus; (**c**) *Spathidium sp.* with its ovoid body, typical of this genus; (**d**) a specimen of the ciliate group Hypotrichia showing the details of the oral structure and associated bristles, scientifically named cilia. (SS, YE)

Microhabitat

As soil dries, the ciliates' habitat becomes restricted to water films on surfaces. They detect prey by chemical-sensing and swim toward the signal, or away from toxic molecules. Their dispersal is by water infiltration through soil pores, or in the air if dry soil is disturbed.

Diversity, abundance and biomass

More than 1 500 species of soil ciliates have been described, but many more remain undescribed so far. One study from Namibia revealed 365 species, of which 128 were new species, from 73 soil samples. Temperate soils typically hold 20 - 30 species per gramme of soil, but most are inactive. In moist soils with plenty of bacteria or prey, there can be 10 000 active cells per gramme declining to none in very dry soils. Although the biomass of ciliates per gramme of soil is very low, when active they can ingest several hundred bacterial cells per minute.

Stramenopiles

Morphology

Stramenopiles are unicellular organisms with two cilia that beat in different directions: a front one that includes tiny hairs (visible on electron microscope images) that pulls the cell, and a trailing one that pushes the cell. In some groups, however, the trailing cilium is missing. Other groups are usually filamentous and only the dispersal cell is ciliated. Terrestrial species form resting cysts in the soil, and in some sexual species dispersal spores are produced after sexual reproduction. [32, 33]

Taxonomy

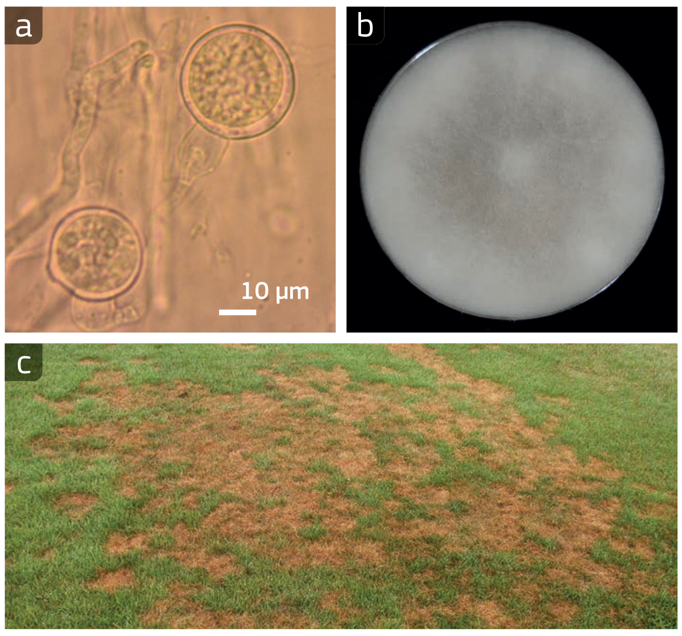
This supergroup includes the brown algae and several groups previously thought to be fungi, such as Hyphochytriales and Peronosporomycetes, which are commonly found in soils. Some species of true brown algae occur in alpine soils (for example, *Vaucheria*), but they are typically rare or absent. Most terrestrial species have lost the ability to photosynthesise (see box on page 35) and appear colourless. They absorb nutrients from the living or decomposing tissues into which they grow.

The *Irish Potato Famine*

- The *Irish Potato Famine*, a period of mass starvation, disease and emigration in Ireland between 1845 and 1852, was caused by *Phytophthora infestans*, a Peronosporomycetes.
- Originally from the Toluca Valley in Mexico, once introduced through infected potatoes, it spread rapidly to much of northern and central Europe.
- Because prior to 1980 they were considered to be fungi, we still lack an effective chemical compound to treat stramenopile parasites since fungicides (aiming to disrupt fungi) do not work.

Microhabitat

Hyphochytriales are found in moist soil environments. They absorb dissolved nutrients with a network of filaments that extend from the cell. Terrestrial species of Peronosporomycetes are decomposers of organic matter or live as plant parasites. They feed by extending filaments into plant tissues. They are economically important because they include species that cause some of the most damaging plant diseases, such as *Pythium* (which causes the damping-off disease in greenhouses), downy mildews and white blister rusts. Diatomea are typically aquatic species that can be found in riparian or regularly flooded soils, and sometimes inside rotting tree logs. Their role and presence in soils is poorly documented. The motile stage is usually a small swimming cell with two cilia, while sexual reproduction leads to the growth of a thick walled spore for dispersal.



(**a**) The structures producing spores, sporangia, of *Pythium aphanidermatum*. (**b**) In the laboratory it is possible to grow *Pythium aphanidermatum* and see its filamentous root. (**c**) *Pythium* species are responsible for plant diseases, such as the 'Pythium blight', a highly destructive turfgrass disease. (LG, JKA)

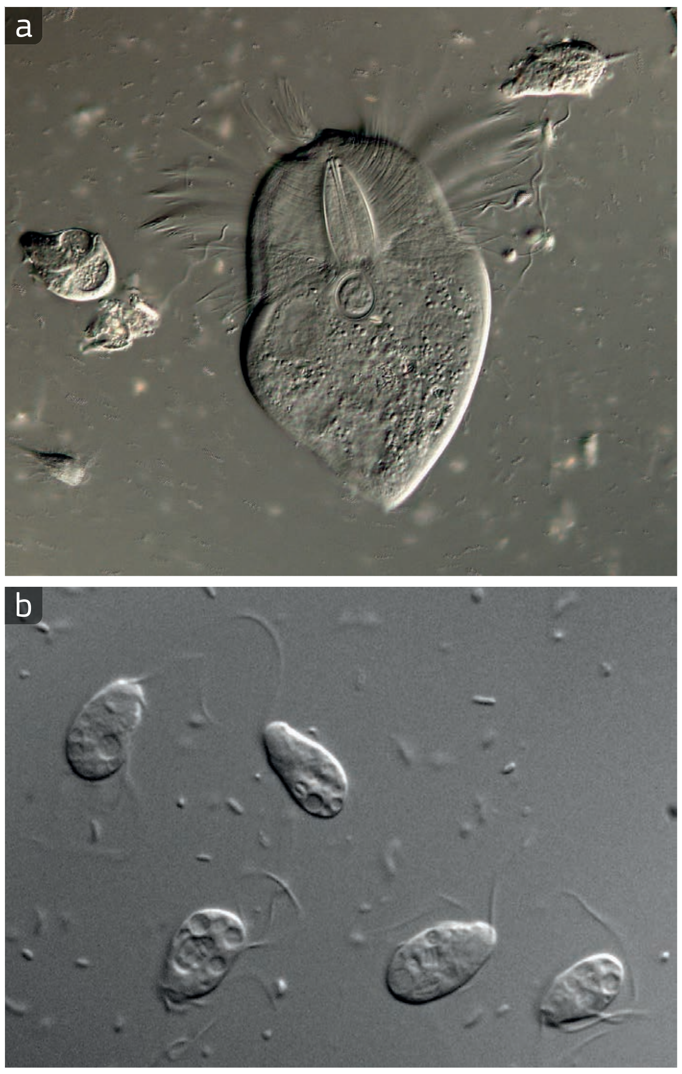
Diversity, abundance and biomass

Only approximately 25 genera of Hyphochytriales are known to science, but many still remain to be described. Fewer than 700 species of Peronosporomycetes are described, but there are likely to be 1 000 - 10 000 species.

Excavata

Morphology

The general body-type in this very diverse group is a small cell with a cilium directed backwards that generates locomotion and directs food (mostly bacteria) toward a feeding groove on the ventral surface, as observed in Fornicata. Many groups have reduced mitochondrial function and prefer micro-aerophilic (low oxygen) or anaerobic (no oxygen) environments. In contrast to many Excavata groups, the Kinetoplastea (commonly called kinetoplastids) have a characteristic mitochondrion with a large amount of DNA. Many kinetoplastid species rely on dissolved nutrients for food (they are osmotrophic). In Parabasalia, the single body-type is replicated hundreds of times to form large multiciliated cells. Both Parabasalia and Preaxostyla have elaborate supporting cytoskeletal elements that provide shape and assist in locomotion. The Heterolobosea are generally amoeboid species with two or four cilia that are used to move in search of food, but some have lost either the ciliated stage or the amoeboid stage. The Euglenids are typically spindle-shaped cells covered by a flexible pellicle; and they can be photosynthetic or not, with the non-photosynthetic species feeding on bacteria or other protists. [34]



Examples of Excavata: (**a**) Parabasalia shows the cilia arranged in clusters near the anterior of the cell; (**b**) *Monocercomonas* spp. can also be found in the digestive tract of wood-eating insects, such as termites. (VH, IC)

Taxonomy

The Excavata is a supergroup, with genera that occur in soil included in six phyla: Fornicata, Parabasalia, Preaxostyla, Discoba, Heterolobosea and Euglenozoa.

Microhabitat

Heterolobosea are found in every ecosystem but are rarely the dominant protists, except in some disturbed soils. The Euglenida, both photosynthetic and heterotrophic genera, occur in soils that are regularly moist or water-saturated (e.g. in wet soil and in riparian areas). Among the Discoba, some free-living species occur in the order Jakobida, such as those of the genus *Andalucia*.

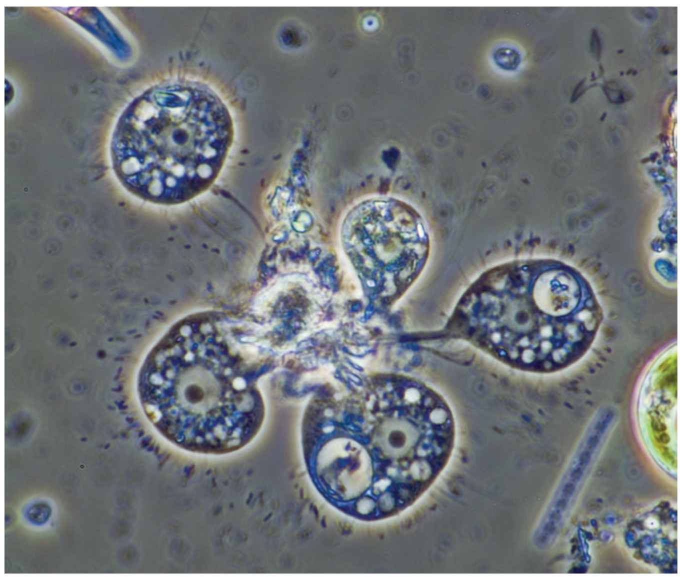
Diversity, abundance and biomass

There are approximately 562 described species of Parabasalia and Preaxostyla, more than 80 species of Heterolobosea and more than 1 520 species of Euglenozoa.

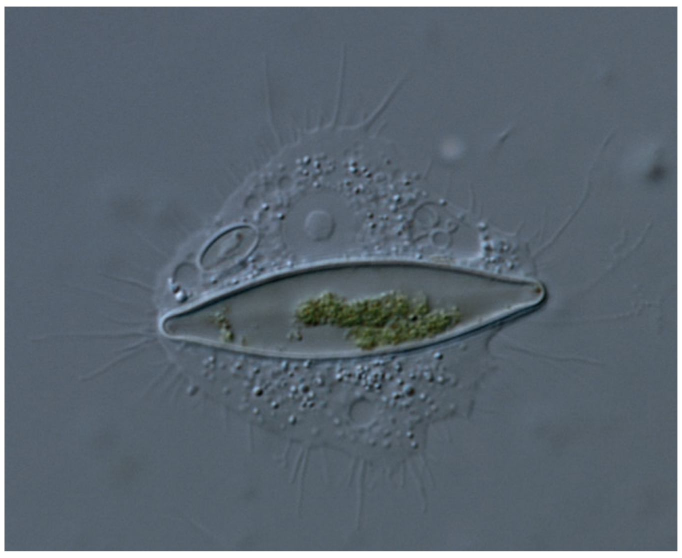
Other protists

Nuclearia, *Ancyromonas* and others

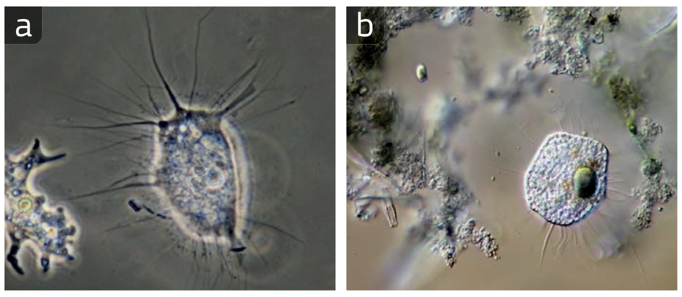
There are several genera that belong to the base of the Opisthokonta, the group that includes animals and fungi. These genera are common in soil, though rarely abundant, and contribute to the ingestion of bacteria. These include *Nuclearia*, *Fonticula*, and the *Rozella*. Several genera found in soils cannot yet be placed into our classification system. They are placed as *incertae sedis* in the eukaryotes. These include *Ancyromonas*, *Breviata* and Apusomonadida.



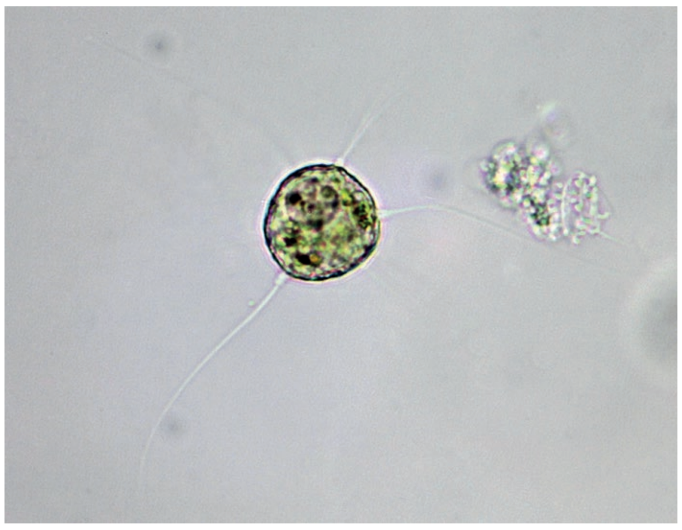
Five specimens of *Nuclearia thermophila* probably feeding on the same prey. This species can be found in peat bogs. (FS)



A species of *Nuclearia* with ingested diatom. (YE)



Diversity of the genus *Nuclearia*: (**a**) *Nuclearia flavocapsulata* usually feeds on bacteria, algae, or detritus; (**b**) *Nuclearia delicatula* feeds by penetrating damaged or old cells of algae or by actively ingesting bacteria. (FS)



A specimen of *Artodiscus saltans*. It can be found in sediments of clear lakes and rivers. Its presence has also been reported in flooded pastures. (FS)

Fungi – Macrofungi

Morphology

Within the fungus kingdom, macrofungi are a group that form visible, often coloured, cup- or cap-like structures (scientifically known as 'fruiting bodies' or 'sporophores') that emerge from the soil. These fruiting bodies are where the spores are formed. The spores are small (1 - 100 μm), usually single-celled, reproductive structures able to tolerate unfavourable growing conditions (e.g. drought). Below the fruiting bodies, each fungus has a mass of hyphae, the typical branching thread-like filaments produced by most fungi. The mycelium is made up of the mass of these hyphae and is responsible for its growth. In the case of soil macrofungi, a large portion of the mycelium is hidden since it grows belowground. When environmental conditions become favourable, the fungus develops the fruiting body and spores that, once released, disperse through the air, or are carried by insects or water. [35, 36]

The Basidiomycota is a group of fungi that comprises the well known, common mushrooms. Their visible part usually has an umbrella-like shape. (**a**) *Hygrocybe* sp.; (**b**) *Hygrocybe graminicolour*; (**c**) *Cyptotrama asprata*; (**d**) *Gymnopilus purpuratus*. (SA)

Taxonomy

Macrofungi, taxonomically belonging to the subkingdom Dikarya, are classified into two main phyla: Ascomycota and Basidiomycota. The Ascomycota, the largest group of macrofungi with more than 64 000 described species, are usually characterised by a cup-like or disc-like fruiting body (technically known as ascoma), where spores are formed within a typical structure, named the 'ascus'. The Basidiomycota (more than 31 000 described species) mostly have a fruiting body (called basidioma) with an umbrella-shaped cap (known as pileus) borne on a stalk (known as a stipe) where the spores are produced. Other phyla that include soil fungi are Glomeromycota, Zygomycota, Chytridiomycota and Blastocladiomycota (see pages 40-41).

Microhabitat

Macrofungi are found in most terrestrial habitats, from woodlands to grasslands, but they are probably most diverse in forests. They need the right climatic conditions to form fruiting bodies; in particular, moisture to allow their spores to develop. Depending on their functions, they can be defined as saprotrophic, parasitic or mycorrhizal. The saprotrophic species play a key role in the degradation of decaying organic matter (i.e. soil, leaf litter and dead wood). The parasitic (see box on page 33) fungi are responsible for several diseases in plants (see box, next page), animals (mostly invertebrates) and other fungi. The mycorrhizal fungi form symbioses with plant roots, a mutualistic association that is beneficial to both partners (see box, page 33).

The Ascomycota is a group of fungi that usually have a visible part, scientifically defined as the fruiting body, with a cup-like shape. (**a**) *Donadinia nigrella*; (**b**) *Sarcoscypha coccinea*; (**c**) *Phillipsia subpurpurea*; (**d**) *Rhodoscypha ovilla*. (SDA, FF, SA, AV)

Fungi: edible, poisonous, bioluminescent and giant

- There are several edible Basidiomycota and Ascomycota. Mushrooms, such as *Boletus edulis* and truffles (*Tuber* spp., see box on page 40), are consumed in many countries.
- Some Basidiomycota produce deadly toxins, such as amatoxin produced by *Amanita phalloides*. Thirty grammes of this fungus may kill a person; others, such as *Ganoderma lucidum*, are considered medicinal fungi.
- Some Basidiomycota (e.g. species belonging to the genus *Mycena*) are bioluminescent.
- In Hainan Island (southern China) a giant specimen of *Fomitiporia ellipsoidea* (belonging to the group of bracket fungi, also included in Basidiomycota) was found to be 20 years old with an estimated volume of 409 000 - 525 000 cm^3 and a weight of 400 - 500 kg. This represents the largest fungal fruiting body (both in volume and in weight) ever found.

Mycena chlorophos is a bioluminescent fungus that can be found in Asia (e.g. Japan and Sri Lanka), Oceania (Australia) and South America (Brazil). The mechanism underlying the bioluminescence has not yet been fully described. (SA)

Diversity, abundance and biomass

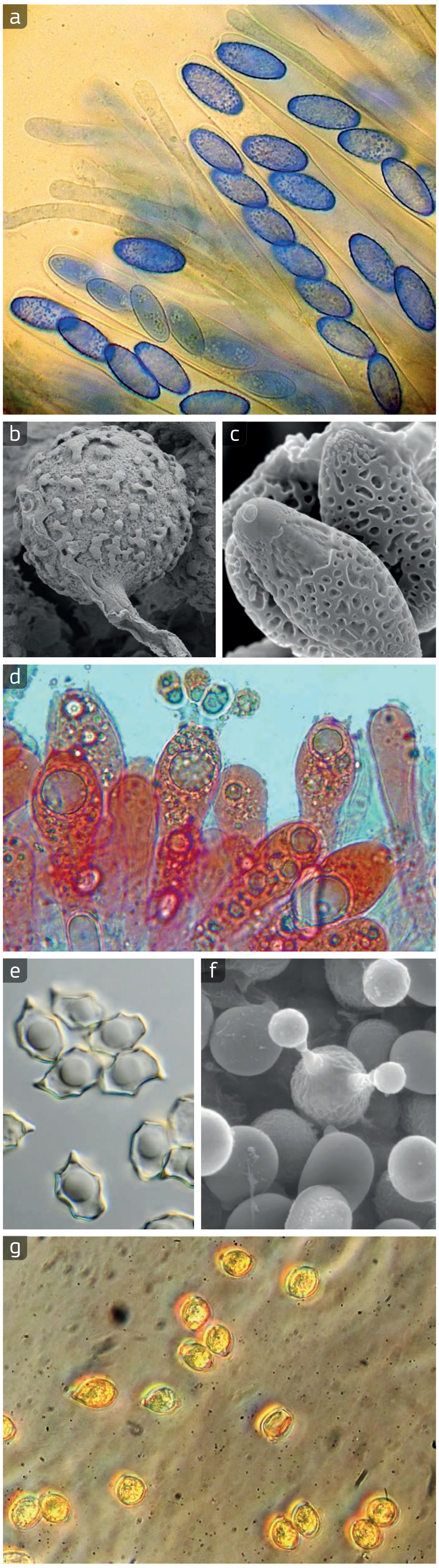
Fungi are extremely abundant. Millions of species have been estimated, but only about 150 000 have been described. Macrofungi have about 90 000 known species. Together with bacteria, fungal hyphae constitute the largest portion of the microbial biomass of soil. Generally, fungal biomass is found to be greater than bacterial biomass in forest soils.

How a fungus is made

Fungal hyphae have a branching structure that resembles plant roots. They allow the fungus to obtain nutrients from the soil. (SA)

- A hypha is a long, branching filamentous structure. In most fungi, hyphae are the main mode of growth, and collectively form the mycelium.
- Hyphae grow at their tips. They can branch through the bifurcation of a growing tip, or through the emergence of a new tip from an established hypha.
- There are different types of hyphae:
  - septate, which have cross walls (called septa) at fairly regular intervals;
  - aseptate or coenocytic, which do not have septa.
- Hyphae can fuse to one another. This process is known as anastomosis.
- Yeasts are fungi that do not have hyphal structures. They are the only unicellular fungi.

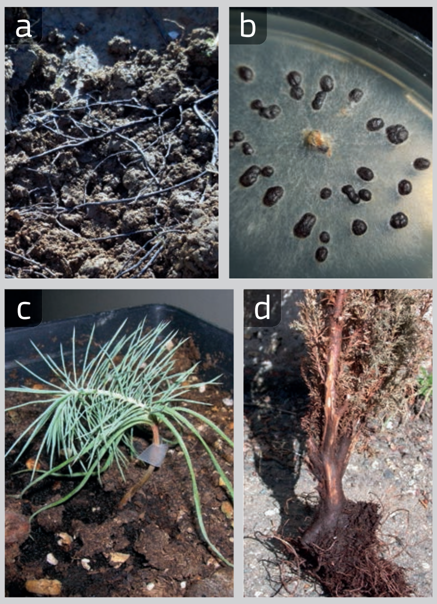
Fungi are very diverse in terms of both shape and colour. Some fungal species showing these aspects are: (**a**) *Leratiomyces* sp.; (**b**) *Geastrum triplex*; (**c**) *Hygrocybe graminicolour*; (**d**) *Cyathus striatus*. (SA)



Spores allow fungi to reproduce. Due to their microscopic dimension, they can easily disperse through air or water. They grow into new individuals under suitable conditions of moisture, temperature and food availability. (**a**) Spores of Ascomycota (blue coloured) develop inside structures called asci; (**b**) electron micrograph of spores from the puffball *Calbovista subsculpta*; (**c**) electron micrograph of spores from *Austroboletus mutabilis*; (**d**) spores of Basidiomycota develop inside structures (red coloured) called basidia; (**e**) spores of *Entoloma* sp.; (**f**) electron micrograph of spores from *Agaricus bisporus*; (**g**) spores of *Botryobasidium aureum*. (LP, SJA, RHL, LP, LK, DEMF, JP)

Soil-borne plant pathogenic fungi

- Soil-borne plant pathogenic fungi (SPPF) comprise organisms that are included in the Fungi kingdom and in the group of fungal-like organisms currently assigned to the Stramenopiles (see page 37). As pathogens, they are responsible for several plant diseases. [37]
- Among fungi, both Ascomycota and Basidiomycota are represented. The major species belong to the genera *Fusarium*, *Phoma*, *Sclerotinia* and *Verticillium* within Ascomycota, and to *Armillaria* and *Rhizoctonia* within Basidiomycota.
- SPPF produce survival structures that may be as simple as cells, called chlamydospores, with a thick wall, or may be more complex like the sclerotia, typical of some fungi (e.g. *Sclerotium*, *Sclerotinia* and *Botrytis*).
- In addition to the survival function, aggregation of hyphae, called rhizomorphs since they resemble plant roots, are typical of species belonging to the fungal genus *Armillaria* and may play a crucial role in fungal spread through the soil, host infection and disease transmission.
- Soil type, pH, water content and temperature of the soil are among the major factors affecting the presence of the soil-borne plant pathogenic fungi.
- *Fusarium* species and *Rhizoctonia solani*, although commonly present in moist soils, tolerate lower water content levels. They also prefer warmer soils (25 - 35 °C).
- SPPF are grouped into two functional categories: soil inhabitants and soil invaders. The first category generally includes unspecialised microbes that infect seedlings and young roots, while the second are disease agents that show a degree of host specificity. Seed decay, damping-off and root rots of seedlings are the most common diseases caused by soil-borne fungi.
- Soil-borne plant pathogenic fungi are reported worldwide in agricultural and forests soils.
- The number of plant pathogenic fungal species on Earth has been estimated to be as high as 270 000; however, the number of SPPF is largely unknown.
- The abundance of SPPF is generally measured as 'inoculum density', which is expressed as the mass, or the number, of spores per gramme of soil. Inoculum density has been reported as ranging from 100 to 10 000 spores per gramme of soil, depending on the species.

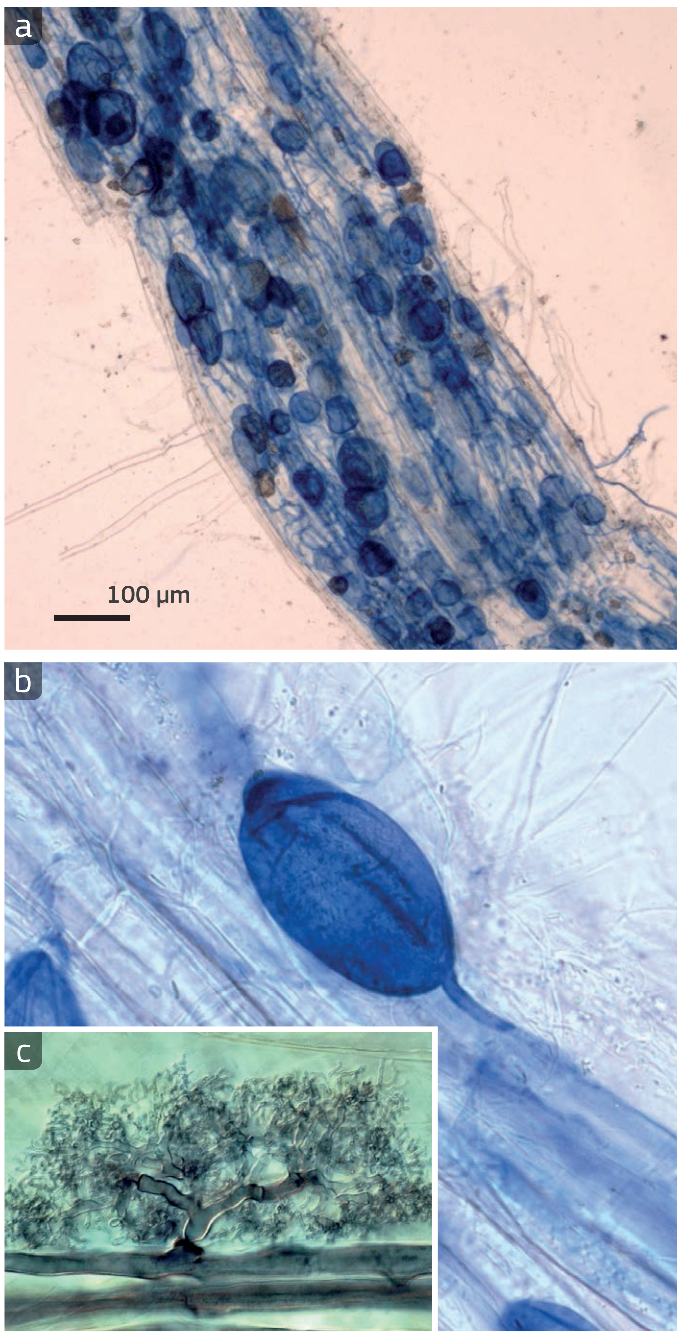


Structures that allow soil-borne plant pathogenic fungi to survive adverse environmental conditions: (**a**) rhizomorphs, as it resembles roots, of the fungus *Armillaria* sp. and (**b**) the black dots are sclerotia of the fungus *Botrytis cinerea*, grown in the laboratory. Diseases caused by soil-borne plant pathogenic fungi: (**c**) damping-off on a stone pine seedling and (**d**) root rot caused by *Phytophthora cinnamomi* on a Port Orford cedar. (LG, PG)

Fungi – Mycorrhizal fungi

Morphology

Mycorrhizas are literally 'fungus-roots' created by symbiotic associations (see box, page 33) between plant roots and fungi. Mycorrhizal fungi help their host plants acquire mineral nutrients from the soil in return for plant sugars. Mycorrhizal fungi form structures outside and inside plant roots. All types form extensive networks of microscopic hyphae that extend outwards from plant roots into the surrounding soil or leaf litter. Arbuscular mycorrhizas (AM), ericaceous mycorrhizas and orchid mycorrhizas are sometimes called 'endomycorrhizas' because the fungi form distinctive structures between and inside the cortical cells of plant roots, but do not generally cause obvious changes in root morphology. By contrast, ectomycorrhizas (EcM) often cause distinct changes to roots that can be observed without a microscope. Reproductive structures also differ among mycorrhizal types. Arbuscular mycorrhizal fungi reproduce with microscopic spores produced in the soil or within plant roots, whereas many ectomycorrhizal fungi reproduce with mushrooms or underground truffles. [38]



Stained roots (**a**) show the colonisation by arbuscular mycorrhizal fungi (AMF). The AMF develop unique structures within root cells: (**b**) vesicles with storage function, and (**c**) arbuscules, the typical brush-like structure which gives the name to this group of fungi. (SLS, MBR)

Diamonds of cuisine

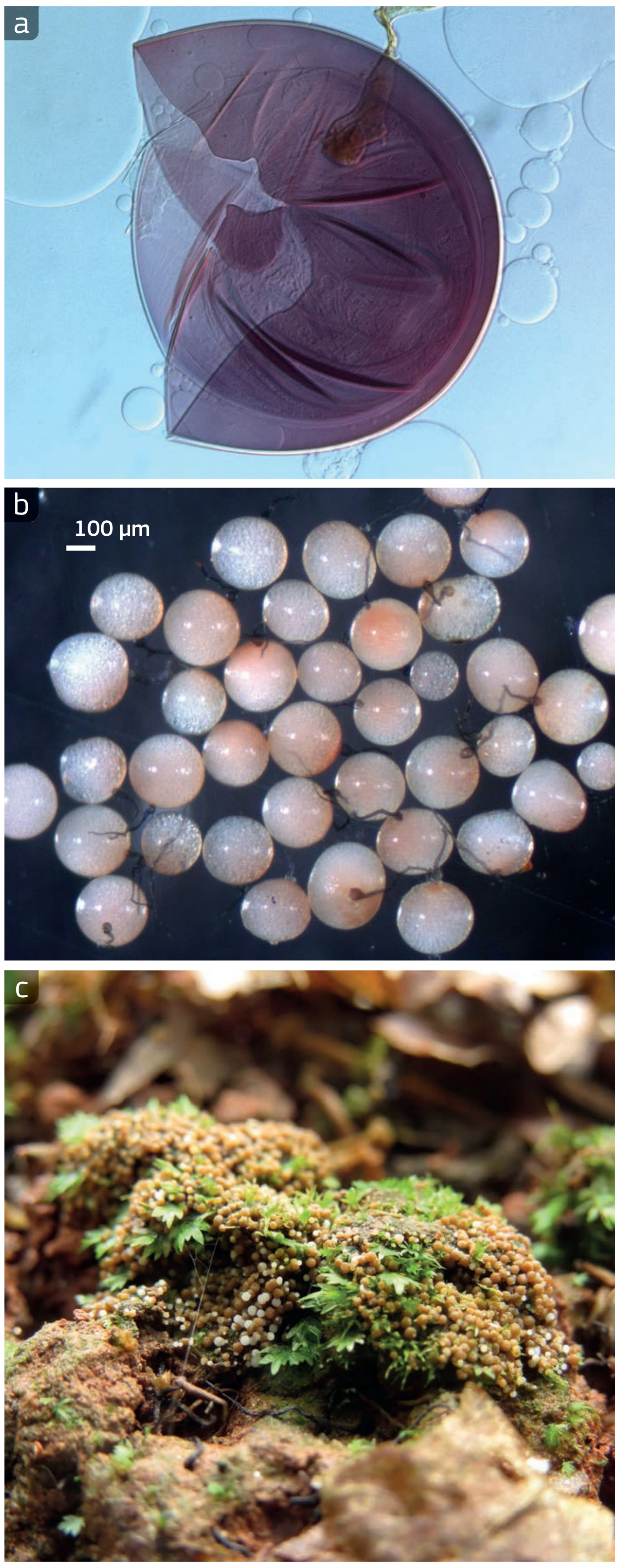
- Mycorrhizas are among the most widespread symbionts in the world. They are found in more than 80 % of all plant species and 92 % of all plant families.
- Mycorrhizas can be managed as biofertilisers as they increase plant nutrient uptake (see pages 98-99).
- Many species of ectomycorrhizal fungi are important culinary mushrooms and truffles.

They look like potatoes but are mycorrhizal fungi. The white truffle (*Tuber magnatum*), known as the diamond of cuisine, is a prized ingredient for cooking. (AO)

The significant mutual benefit of mycorrhizal symbioses is evident from their tremendous abundance and diversity. Mycorrhizal fungi are found in all terrestrial biomes and in association with most plant families. They are found with trees, shrubs, forbs, grasses and agricultural crops. Arbuscular mycorrhizas are abundant in tropical forests, grasslands, savannahs, deserts and arable lands, and ectomycorrhizas dominate temperate and boreal forests. Ericaceous mycorrhizas are common in boreal forests and heathlands. Orchid mycorrhizas are essential to the survival of orchids throughout the world.

Glomeromycota

Fungi in the phylum Glomeromycota form arbuscular mycorrhizal symbioses with the majority of plant species, by colonising the root cortex (see box, page 43) and forming an extensive mycelium, vesicles and arbuscules. This phylum contains 17 genera and 240 species distributed in nine families and four orders. Common genera include *Glomus*, *Rhizopaghus*, *Sclerocystis*, *Gigaspora*, *Scutellospora*, *Cetraspora* and *Acaulospora*. Glomeromycota produce abundant hyphae and spores in soils. In grasslands and agricultural lands, these fungi comprise an estimated 20-30 % of soil microbial biomass, making arbuscular mycorrhizal fungi among the most abundant organisms in many soils.



Arbuscular mycorrhizal fungi reproduce through spores that can have various dimensions and colours: (**a**) a broken spore of *Cetraspora pellucida*, (**b**) the rosy spores of *Gigaspora rosea*, and (**c**) structures producing spores (sporocarps) of the fungus *Sclerocystis coremioides* associated with mosses. (SLS, KK)

Ectomycorrhizas

Approximately 6 000 fungal species establish ectomycorrhizal associations with many species of trees and woody plants. At least 20 families of Basidiomycota (e.g. Amanitaceae, Russulaceae, Boletaceae) and seven families of Ascomycota (e.g. Pezizaceae, Tuberaceae) are known to establish ectomycorrhizas. The biomass of ectomycorrhizal fungi mycelia has been estimated to range from 700 to 900 kg per hectare, and 20-40 % of an ectomycorrhizal root weight is due to the fungus.

Some of the fungi that are found in woodlands are ectomycorrhizal: (**a**) *Boletus bicolour*, and (**b**) *Scleroderma aurantium*. (MW)

Short lateral roots of a beech tree colonised by a white layer of hyphae of the ectomycorrhizal fungus *Xerocomus pruinatus*. (MB)

Ericaceous and orchid mycorrhizas

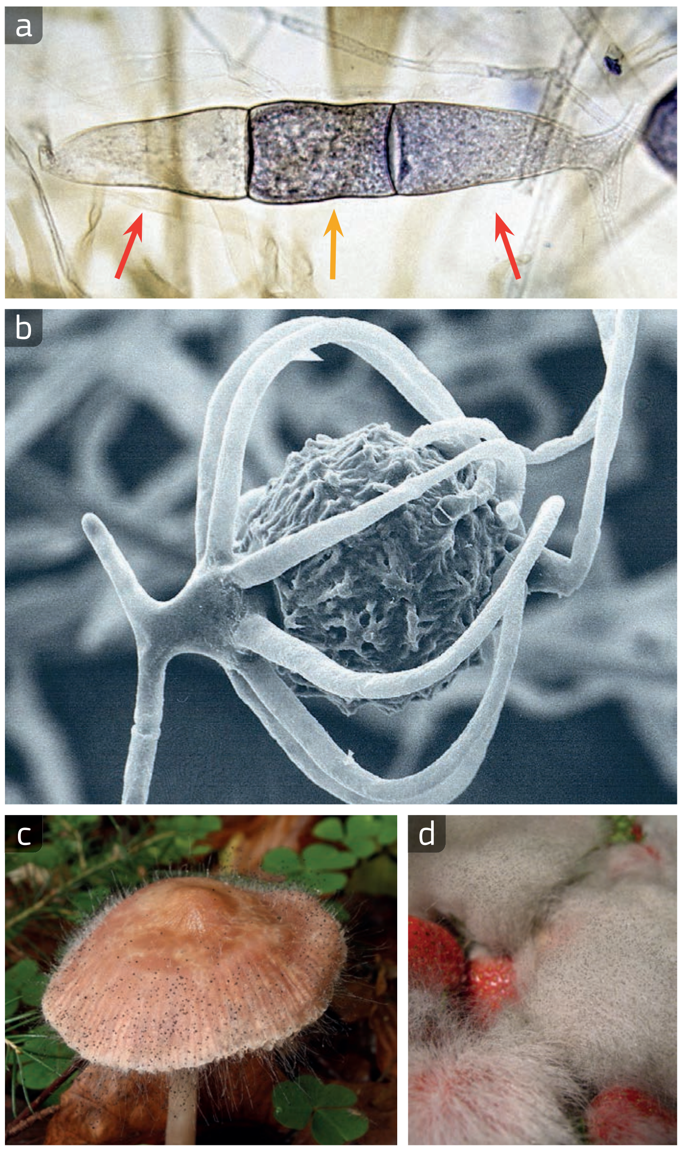
Most plant species belonging to Ericaceae, including the genera *Rhododendron*, *Calluna* and *Vaccinium*, form ericoid mycorrhizas. These plants form delicate roots lacking root hairs and their outermost radical cells become heavily colonised by Ascomycota from the genera *Rhizoscyphus* and *Hymenoschyphus*. Orchid mycorrhizas are established between plant species of the family Orchidaceae (20 000 to 35 000 species) and several groups of fungi in the phylum Basidiomycota, as well as some rare Ascomycota.

Plants belonging to Ericaceae, like heather (*Calluna vulgaris*) and Orchidaceae, may form specific fungal symbioses called ericaceous and orchid mycorrhizas, respectively. (RH)

Fungi – Other fungi

Zygomycota

A unique feature of the Zygomycota is the zygospore, which is formed within a structure called the zygosporangium after the fusion of specialised hyphae called gametangia during sexual reproduction [35, 36]. The mature zygospore is often thick-walled and undergoes a dormant period before germination. Nevertheless, asexual reproduction occurs much more frequently than sexual reproduction in the zygomycetes. During asexual reproduction, hyphae grow over the surface of the material on which the fungus feeds and produce clumps of erect stalks, called sporangiophores. The tips of the sporangiophores form spore-producing structures, the sporangia. Thin-walled spores are produced within the sporangia and are thus shed above the substrate, in a position where they may be dispersed by wind or water, allowing the fungus to spread and colonise new substrates quickly and efficiently. The Zygomycota include two main classes: Zygomycetes (that comprise Mucorales, the most studied order) and Trichomycetes. More than 1 000 species have been described so far. Zygomycetes are commonly decomposers, symbionts or parasites (see box, page 33) in terrestrial habitats. For example, members of the Mucorales are easily isolated from soil, humus and dung. Furthermore, some Mucorales are used to ferment foods and produce important industrial products, such as lactic acid and rennin (used to make cheese). Conversely, some species have a negative economic impact by causing storage rot in fruits. Trichomycetes are obligate associates of arthropods, including insects and millipedes. The host may be an adult or larva, in terrestrial or aquatic habitats. The fungi are usually found attached to the gut lining of the host. The precise relationship is difficult to determine in most cases; however, they often seem to be commensals, doing little or no harm to their hosts, with the fungus gaining nutrients from the gut of the host. Some zygomycota can also be pathogens of animals, plants, amoebae and, especially, other fungi. Of the more than 1 000 species of described Zygomycota, the majority are found in soil, with some genera (*Mucor, Mortierella* and *Rhizopus*) that are extremely common and reported in almost all surveys of soil fungi.



(**a**) Once the hyphae of two opposite mating types (red arrows) have made initial contact, they give rise to a young zygospore (orange arrow). (**b**) A highly ornamented mature zygospore held by hyphae. (**c–d**) Zygomycota can attack other fungi and fruits. (GB, HK, CSI)

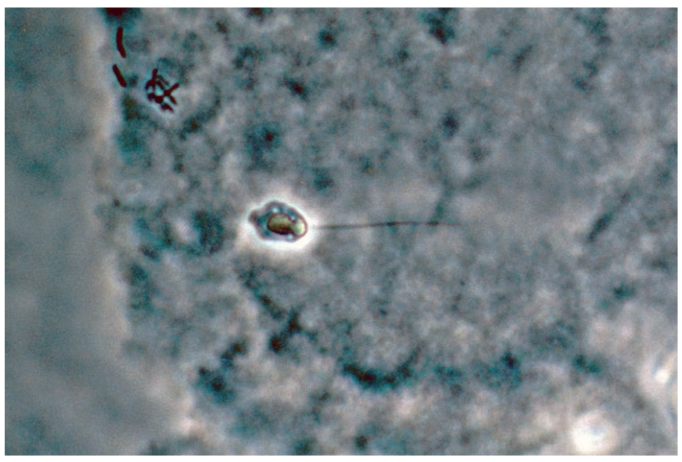
The hat thrower

- A unique spore dispersal strategy for the Zygomycota of the order Mucorales is exhibited by the dung fungus of the genus *Pilobolus*.
- Its name literally means 'the hat thrower'. When spores are ready, the turgor pressure within the vesicle beyond the sporangium (spore-producing structure) builds to a sufficient level that allows the sporangium to be launched. The entire black sporangium is explosively shot off up to distances of several metres.
- For an organism less than 1 cm tall, this involves acceleration from 0 to 20 km/h in only 2 µs, equivalent to a human being launched at 100 times the speed of sound (more than 120 000 km/h).

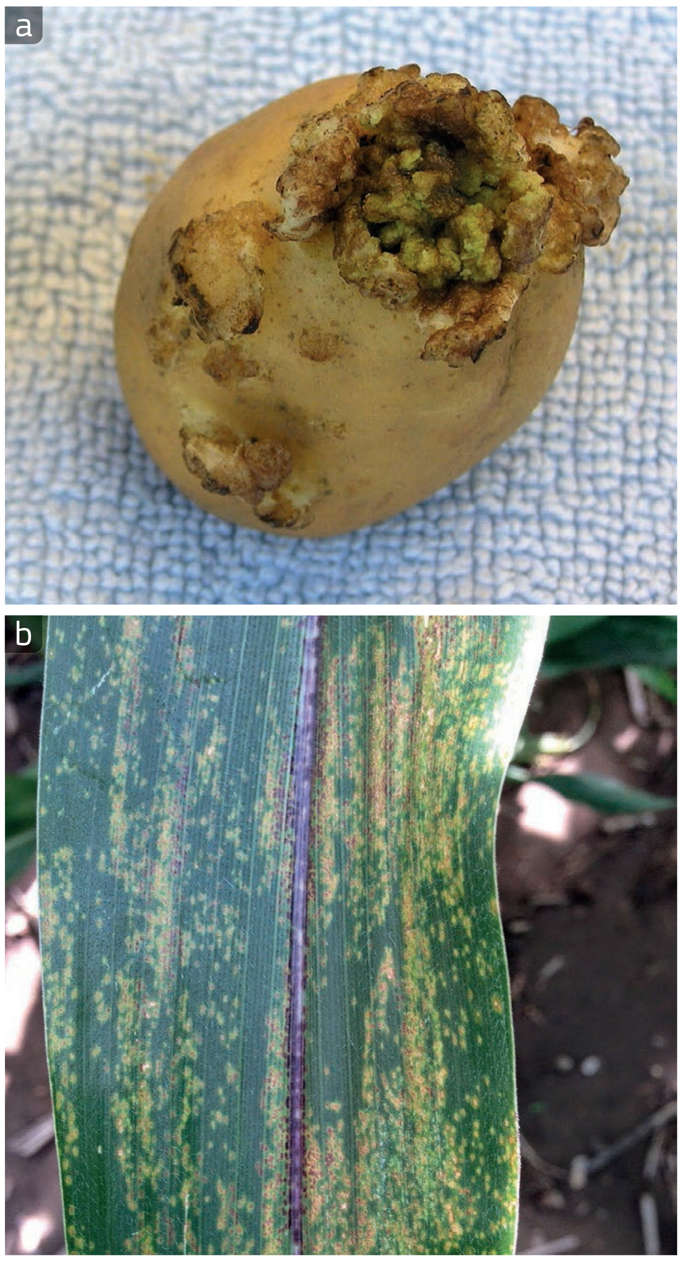
A species of *Pilobolus* showing a black sporangius that will be launched several metres away to disperse the spores. (RK)

Chytridiomycota

Chytridiomycota (chytrids) are characterised by their asexual state, a motile (capable of moving) zoospore with a single whiplash flagellum oriented and located posteriorly [35, 36]. Zoospores are released through an opening in the wall, and their release usually indicates the death of the 'body' of fungus, called thallus. They are the only fungi that form flagellate spores. Chytridiomycota are typically unicellular, with limited hyphal growth in some cases. Chytrids require a water film in which zoospores can swim until a desirable substrate is found. For this reason, chytrids are usually regarded as aquatic fungi, although those that thrive in the capillary network around soil particles are typically considered terrestrial. Approximately 700 species of chytrids have been described, including species living in temperate forest and rainforest soils. Soil chytrids include plant pathogens and vectors of plant viruses such as *Synchytrium endobioticum,* which causes the potato wart disease (black scab) and serious commercial damage. Some chytrids are nematode (see pages 46-47) and algae parasites. As Chytridiomycota often feed on decaying organisms, they are also important decomposers. These organisms are responsible for the decomposition of resistent materials, such as pollen and cellulose. This colonisation of pollen usually occurs during the spring when bodies of water accumulate pollen falling from trees and plants. Estimates of the number of chytrid species occurring in soil are currently unavailable.



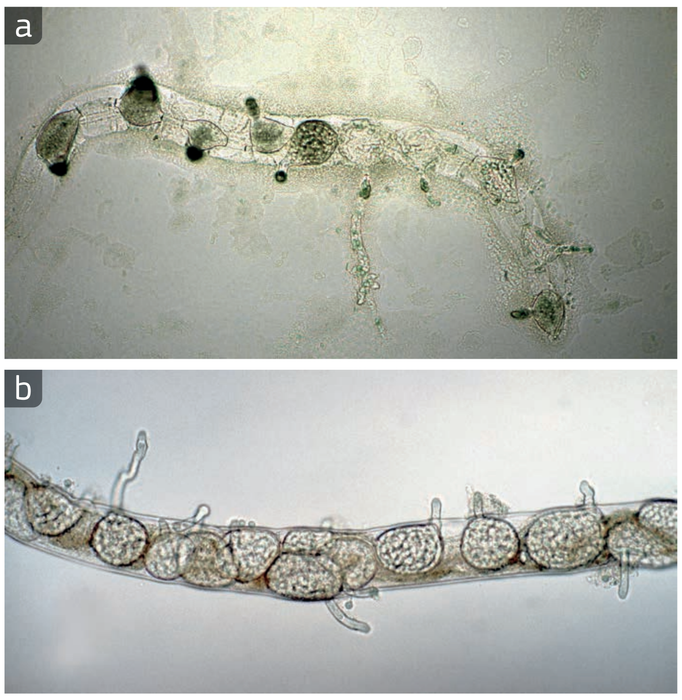
A zoospore with its flagellum (thin dark line) allowing it to move. Chytridiomycota and Blastocladiomycota are the only fungi producing this type of spore. (GB)



Chytridyomycota and Blastocladiomycota are responsible for some plant diseases: (**a**) potato wart disease caused by the chytrid *Synchytrium endobioticum* and (**b**) brown spot disease brought by the blastoclad *Physoderma maydis* on maize. (SK, mm, SPR)

Blastocladiomycota

The Blastocladiomycota (blastoclads) are one of the currently recognised phyla within the Fungi kingdom. Blastoclads were originally the order Blastocladiales within the phylum Chytridiomycota, until molecular and zoospore structural characters were used to demonstrate that it was a group separated from chytrids. Similar to Chytridiomycota, Blastocladiomycota produce zoospores to colonise new substrates. Furthermore, members of Blastocladiomycota are capable of decomposing complex materials, such as cellulose and chitin. Of economic importance is *Physoderma maydis*, a parasite of maize and the causal agent of brown spot disease. There is a blastoclad, *Sorochytrium milnesiophthora*, that is a tardigrade parasite (see page 44). However, the best known species, belonging to the genus *Catenaria*, are nematode parasites. As they are mainly known to be aquatic fungi, a reliable evaluation of their abundance in soil is not available.



(**a**) The blastoclad *Catenaria anguillulae* living inside a nematode, which it has parasitised. (**b**) The spore-producing structures (sporangia) of *Catenaria* emerge from an infected nematode. (EK, GB)

Photosynthesisers – Lichens

Morphology

Lichens originate from symbiosis, involving a fungus 'mycobiont' (the dominant partner) and one or several photosynthetic 'photobionts' (the energy producers), either unicellular green algae, cyanobacteria (see page 35) or both. The symbiosis is mutualistic since the fungus benefits from the food (carbohydrates) produced by algae or cyanobacteria, and the algae or cyanobacteria benefit by being protected from the environment by the fungus. This symbiosis is also cyclical as the two partners must activate the association with every new generation. Also, specific bacterial communities are obligate lichen symbionts and, therefore, considered to be an integral part of lichen structure. The thallus is the vegetative and assimilative body that relies on the interactions among the symbionts. The thalli (growth forms) can vary from discrete granules of 0.5 - 50 mm to pendent lichens of 2 m in length, and have an extraordinary range of growth types, each of which show particular adaptations to different environments. [39]

Cladonia diversa is a lichen with composite thalli of scales (basal part) and scyphi (erect). Lichens are the result of a symbiotic relationship between an alga or a cyanobacterium (or both) and a fungus. This relationship is beneficial to both the partners. (JDF)

Taxonomy

Lichens are derived from the fusion of two unrelated groups of organisms, where the taxonomy of the resulting hybrid organism is based on the fungus. Ninety-eight percent of lichenised fungi are Ascomycota in 18 of the 45 recognised orders (only five contain exclusively lichenised taxa), and two percent are Basidiomycota (see pages 38-39). The lichenised green algae are placed in Trebouxiophyceae (Chlorophyta), while cyanobacteria comprise several orders.

Microhabitat

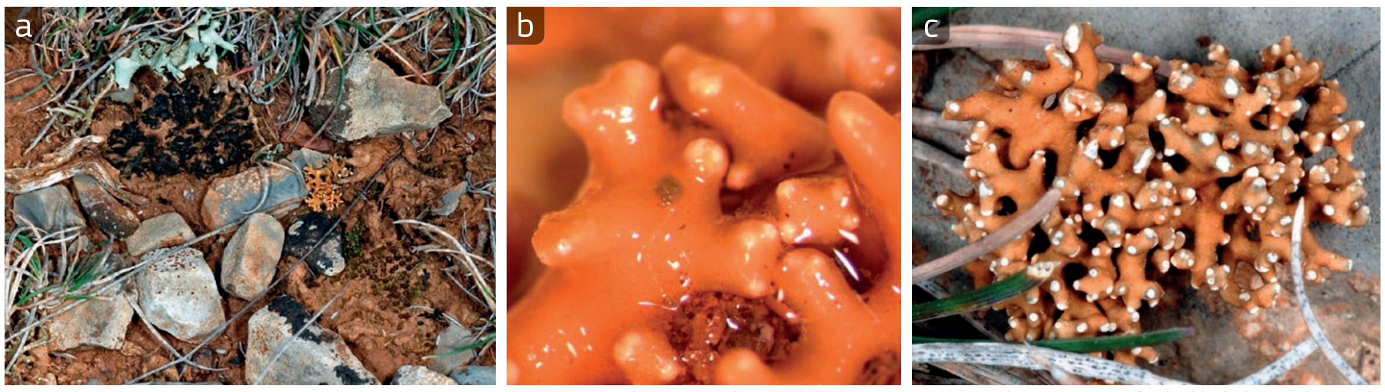
Lichens growing on the ground are 'terricolous' or 'epigeous' and colonise a wide range of soils. The habitats include: mineral or organic soils, thin layers of strongly weathered rocks, rock crevices, sand dunes, grasslands, bryophytes (i.e. mosses, hornworts and liverworts), damp trunks or rocks, peatlands and rotting wood. In tundras, cushions of 'reindeer lichens', mostly *Cladonia* species, are basic food for these herbivores. Continental steppes harbour specialised types of erratic vagrant thalli that allow them to disperse easily. Lichens are a major component of biological soil crusts (see page 73) in desert and dryland regions, growing in patches that increase soil stability and permeability, as well as resist erosion.

Diversity, abundance and biomass

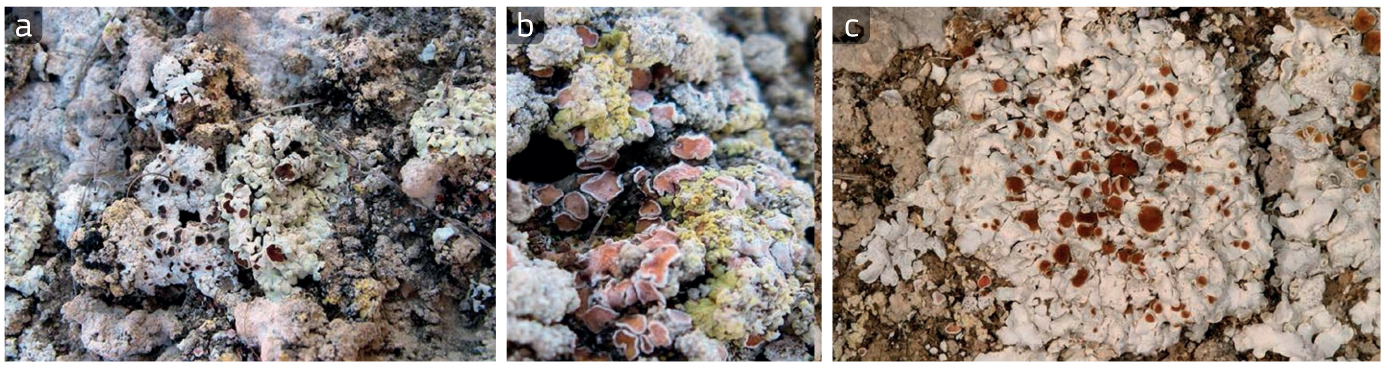
There are about 28 000 species living in all types of habitats. Only 5 - 12 species thrive in tundra or desert soils, while in tropical areas, rocks and bark surfaces may support more than 50 species in less than 0.5 m^2.

Uniqueness of lichens

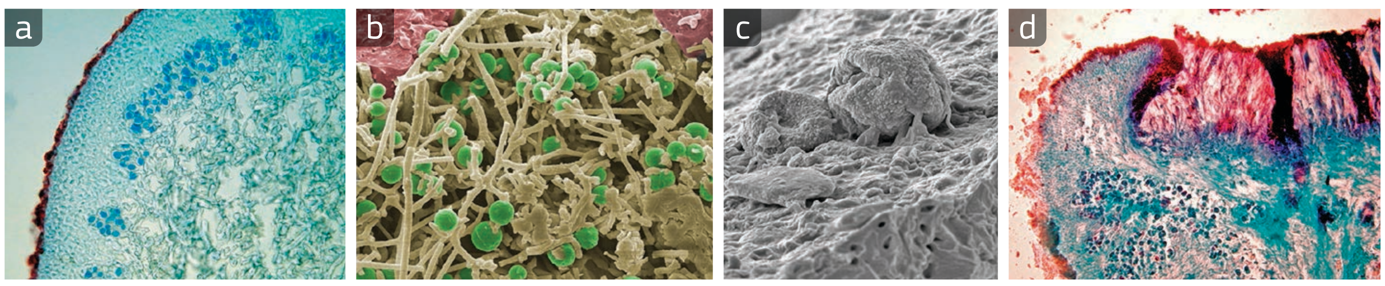
- Lichens are complex and unique entities with characteristics not found in either the original fungi or algae. These include slow growth, long life, ability to revive from severe desiccation, high habitat specificity, tolerance to extreme temperatures and the ability to survive on all types of substrata and habitats.
- Some rock-inhabiting species are among the oldest living organisms on Earth.
- Lichens are extremely vulnerable to habitat alteration and are effective 'early warning indicators' of environmental changes.



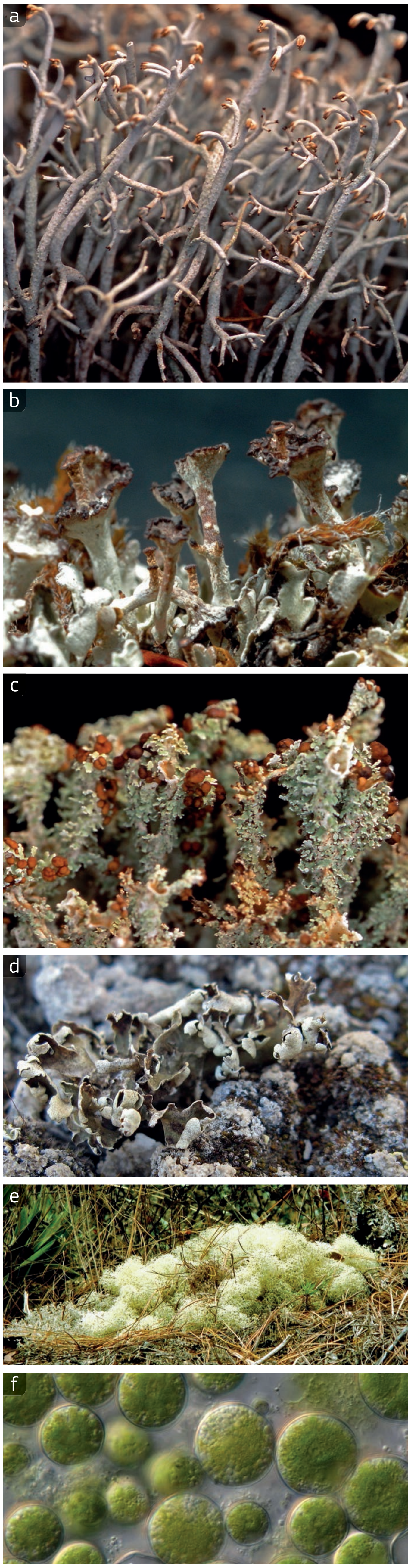
(**a**) Community of vagrant and erratic lichens in continental, windswept steppes; (**b**) the black dot is a bacterial community living on a lichen; (**c**) a specimen of *Circinaria fruticuloso-foliacea* with its shrubby aspect. (EB, CS)



Biological soil crust on semi-arid soils: (**a**) lichen community of *Acarospora nodulosa* and *A. placodiiformis* growing tightly appressed to the gypsum soil (crustose growth); (**b**) the pink sqamulose *Psora decipiens*, and the yellow *Fulgensia desertorum*; (**c**) the placodioid *Squamarina lentigera* that radiates out from the centre. (EB, SPO)



Lichen anatomy: (**a**) light microscopy of the undifferentiated body (thallus) of *Circinaria fruticulosa* with a dark layer of soil particles; (**b**) thallus layer with fungus and algae (green spheres); (**c**) symbiotic bacteria growing on a lichen; (**d**) reproductive structure (apothecium) of the mycobiont in the lichen *Acarospora nodulosa*. (EB, FGB)

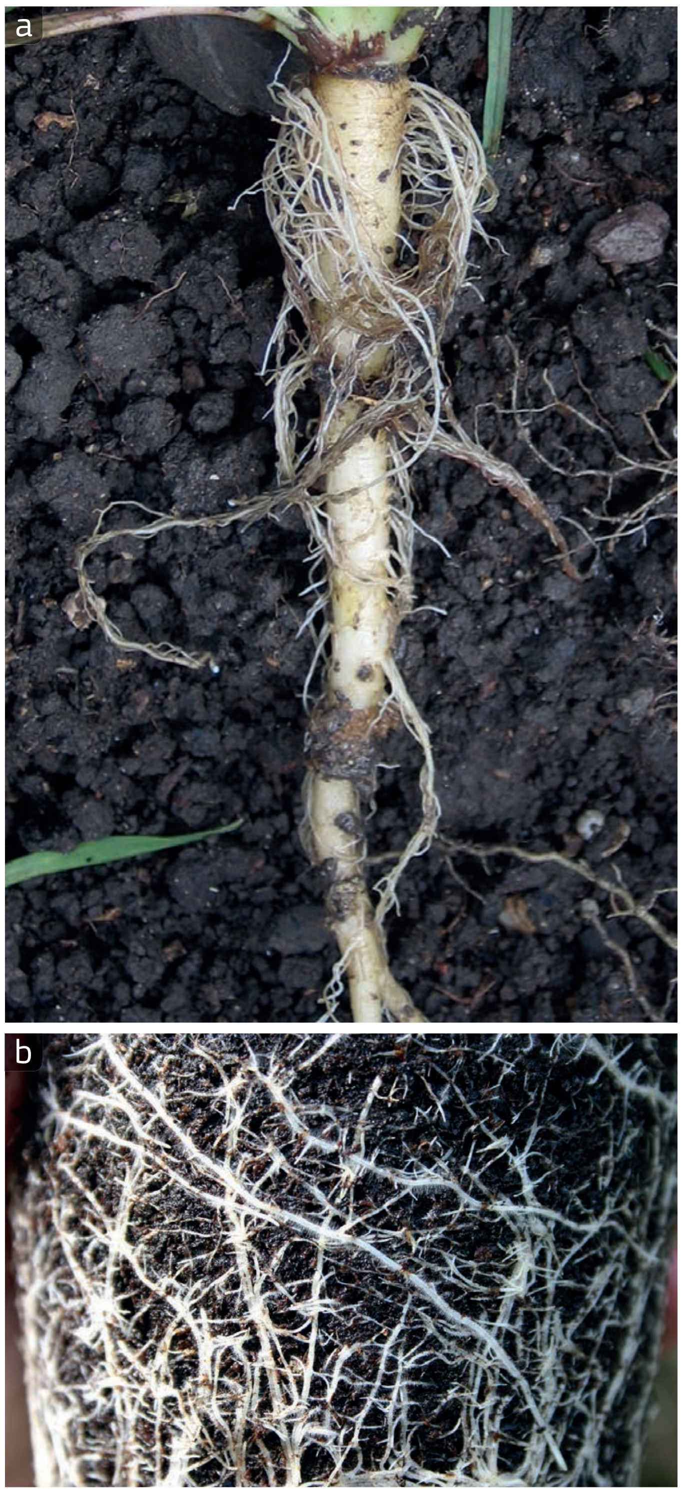


Diversity of the lichen genus *Cladonia*: (**a**) *C. rangiferina*; (**b**) *C. cervicornis* subsp. *pulvinata*; (**c**) *C. squamosa*; (**d**) *C. convoluta*; (**e**) *C. confusa*; (**f**) *Asterochloris mediterranea*, a common alga in the genus. (SPO, EB)

Photosynthesisers – Plants

Morphology

Plants are organisms that have a visible part aboveground (the shoot system) and a hidden part belowground (the root system). The extreme variety in the shapes of the visible portion of the plants is also present in the roots below the surface of the soil. The two main types of root systems are fibrous and taproot. Fibrous roots are the traditional structures formed by primary and secondary roots branching in all directions in the soil. By contrast, taproots are characterised by a single firm root growing straight down, with minor roots developing either side of it. Other specialised roots do exist; for example, the tuberous roots of sweet potato are modified for the storage of nutrients and water, while the stilt roots of mangroves allow the plant to be stable in wet and muddy soils by cropping up from the trunk and growing downwards. Roots are usually covered by root hairs that are invisible to the naked eye and form a large surface area allowing plants to take up water and mineral nutrients from the soil. [40, 41]



Plants can have two main types of root system: (**a**) taproot with a large, central and dominant root or (**b**) fibrous with many branched roots. (SPS, BL)

Taxonomy

Green plants (Viridiplantae), are a kingdom of organisms including from 300 000 to 315 000 different species. The majority, 260 000 to 290 000 species, produce seeds. The two main groups of seed plants are the flowering plants (Angiosperms) and the naked-seed plants (Gymnosperms). Angiosperms produce fruits containing seeds and include the most common vegetables and fruits used as food by humans. Angiosperms comprise monocotyledons (e.g. grasses, such as maize or wheat) that have fibrous root systems, and dicotyledons (e.g. carrots and apples) that have taproot systems. Gymnosperms include the conifers, which are woody plants with cones and root structures similar to those of dicotyledons.

Microhabitat

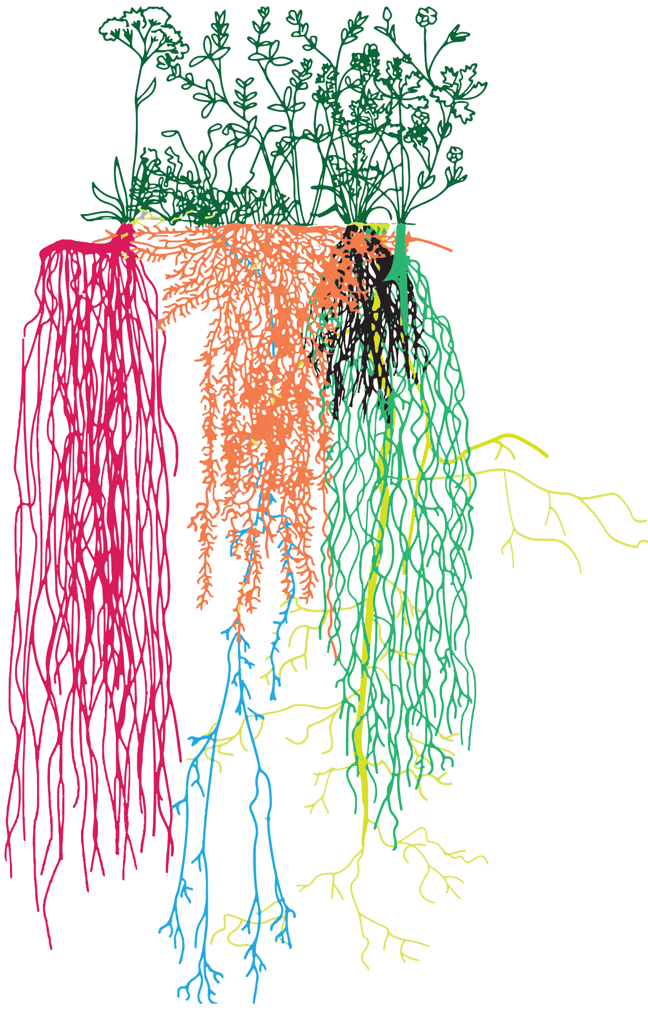
Plants are found everywhere, from tundra to desert. The aboveground parts of plants are responsible for the photosynthesis (see box on page 35) that provides energy for the plants and replenishes oxygen in the atmosphere. By contrast, the root system has three main functions: 1) absorption of nutrients and water; 2) anchorage to soil; 3) storage of nutrients. Plant roots generally grow anywhere with suitable environmental conditions and readily explore soil macropores (see page 72). The part of the soil that is directly influenced by roots is called the rhizosphere, and is very rich in soil microorganisms (e.g. in bacteria and fungi).

Diversity, abundance and biomass

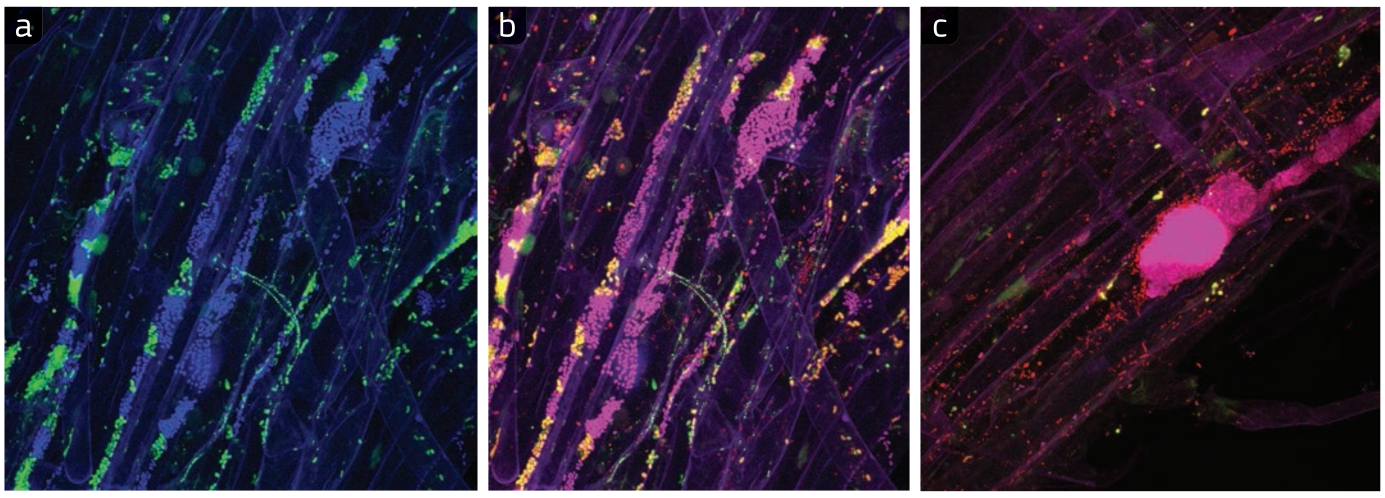
The number of known plant species has been estimated to be around 400 000. The majority (i.e. 260 000 - 290 000 species) belong to seed plants with around 1 000 Gymnosperms. Nearly all the others are classified as flowering plants (Angiosperms). It is difficult to estimate plant root biomass because: 1) the fine roots are difficult to sample and 2) the separation of living from dead roots is very tedious. Nevertheless, as a general rule, plants allocate relatively more biomass to roots if the limiting factor for growth is belowground (e.g. water), while they allocate relatively more biomass to shoots if the limiting factor is aboveground (e.g. light). For this reason, a low root biomass is usually typical of plants living in forests and woodlands, while a higher root biomass can be found in desert plants.

Incredible numbers of plant roots

- The maximum rooting depth, 68 metres, was found in a plant in the Kalahari Desert.
- A single winter rye plant (*Secale cereale*) can grow roots measuring 620 kilometres in only 0.5 cubic metres of soil.
- A grove of over 40 000 clonal quaking aspens (*Populus tremuloides)*, located in south-central Utah (USA), has the largest root system in the world. It is estimated to weigh 6 600 tonnes.



Plant roots can have different traits. Architectural traits determine the spatial configuration of the entire root system and include rooting depth, root length density and root branching. Morphological traits refer to features of individual roots, such as root diameter and specific root length. Biotic traits involve direct interactions between roots and soil biodiversity, such as associations with mycorrhizal fungi and rhizobia (see pages 33-34), but also interactions with pathogens (see box on page 39) (derived from Bardgett *et al.*, Trends in Ecology & Evolution, 2015). (LM) [42]

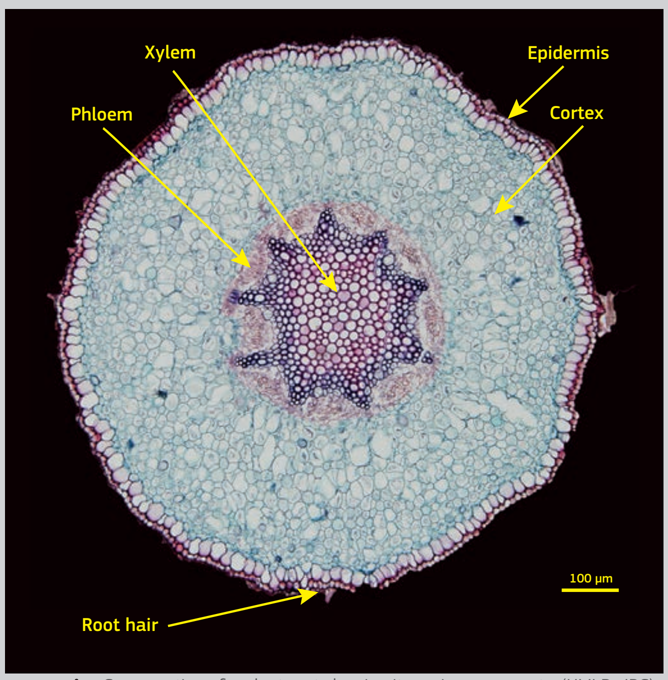


Microbial interactions in the rhizosphere. The three images were taken with a confocal microscope and show the microbial colonisation of a lettuce (*Lactuca sativa*) root by the native bacterial community. (**a–c**) Different colours correspond to different groups of bacteria. Different microbes do not share habitats, but rather colonise different areas of the rhizospere, avoiding each other. (MC)

Root structure

Observing a cross section of a plant root, the main visible structures are:

- root hair: they have fundamental importance in absorbing water and nutrients and in attaching the plant to the soil or other growing surface. They are lateral extensions of a single cell;
- epidermis: a single-layer group of cells that forms a boundary between the plant and the external environment. Its functions are: protection against water loss, regulation of gas exchanges, and absorption of water and mineral nutrients;
- cortex: formed by unspecialised cells lying between the epidermis and the vascular, or conducting, tissues (xylem and phloem). These cells can be colonised by symbiotic fungi (see page 40). In some plants, such as carrots, the cortex becomes a storage organ;
- phloem: conducts products of photosynthesis (i.e. sugars – see box on page 35) from leaves to roots;
- xylem: conducts water and minerals from the roots up through the plant.
- Typical roots contain meristematic, elongation, and differentiation zones. In the meristematic zone, cells undergo rapid division, creating new cells for root growth. These cells begin to elongate (elongation zone), giving the root added length. The zone of differentiation contains mature, specialised cells, such as phloem, xylem, and root hairs.



Cross section of a plant root showing its main components. (UMLD, JRC)

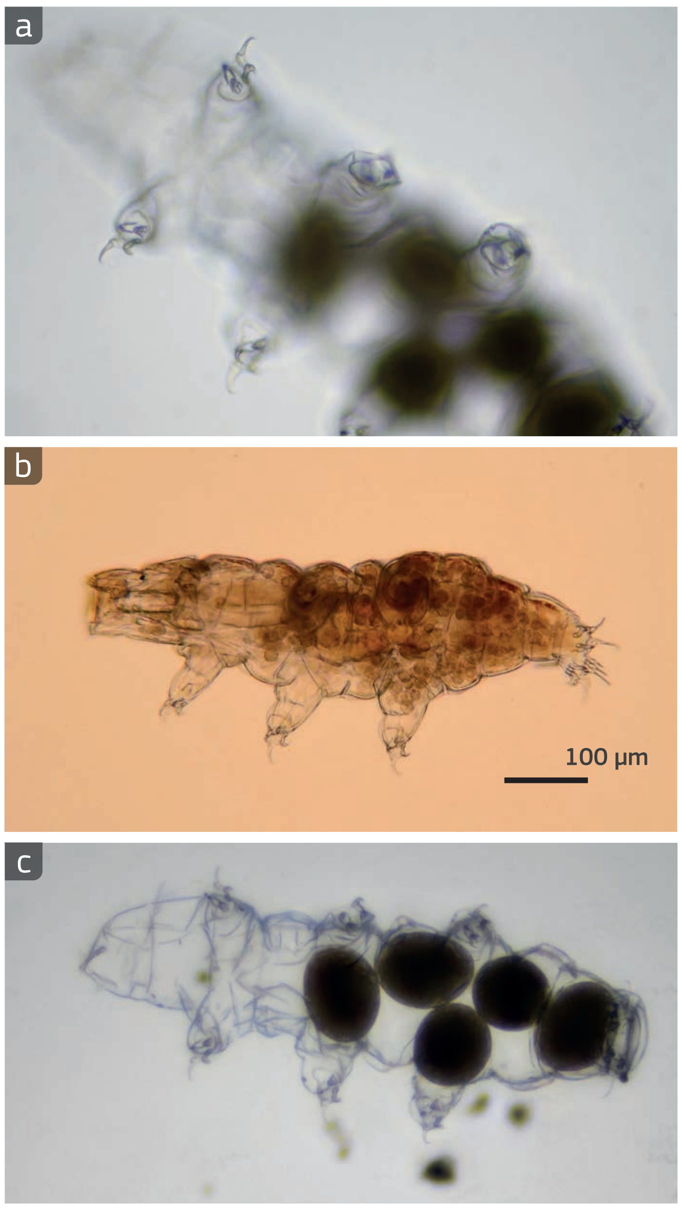
Microfauna – Tardigrada

Morphology

Tardigrades are microscopic animals (0.1 - 1.7 mm) that are strongly dependent on the availability of water to permit gas exchange and avoid desiccation. This led to their original name 'little water bears', which was given to them by the German pastor J.A.E. Goeze, who first described them in 1773. Their bodies are short, slightly segmented and equipped with eight poorly articulated legs ending in four to eight claws. They move very slowly, in a manner similar to that of a bear. All tardigrades possess an eversible buccal tube and two stylets to pierce animal or plant cells, and a pumping pharynx to suck out their internal fluids, although some species are carnivorous and consume rotifers and nematodes (see pages 45-47). The morphology of the claws, cuticle (outer covering) and the buccal apparatus (mouth) is used to identify the different species. [43, 44]

Tardigrades in space!

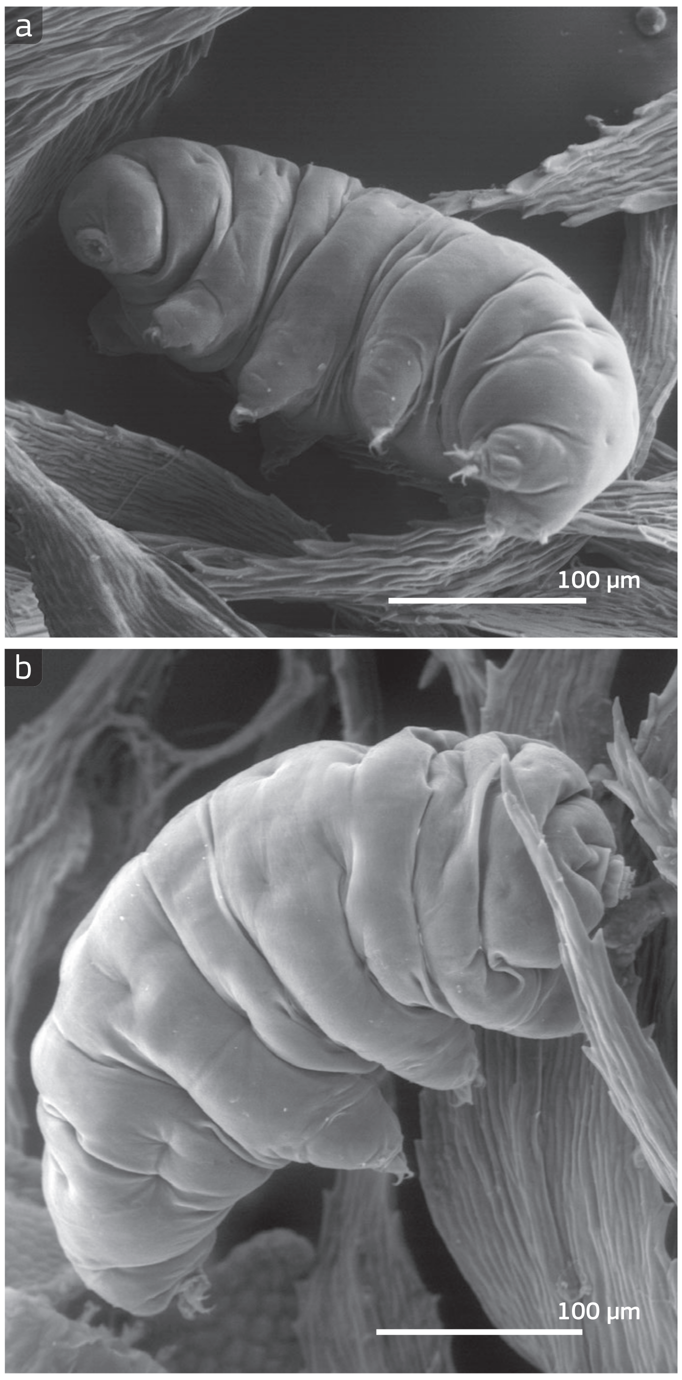
- Their resistance to cosmic radiation and vacuum has led tardigrades to be part of several space expeditions: the TARDIS project in 2007, as part of the Russian FOTON-M3 mission, which was sponsored by the European Space Agency (ESA), and the Tardkiss experiment in 2011, which included the BIOKIS Project, sponsored by the Italian Space Agency.
- The revelation that these tiny animals survived exposure to the harsh space environment has given further support to the 'panspermia theory'. This old idea holds that 'seeds of life' could have spread between planets and, for some, represents a possible origin of life on Earth. So could these eight-legged creatures have travelled through space to eventually colonise other planets, such as our Blue Planet?
- They are the toughest animals on the planet, able to withstand a dose of 5 000 grays of gamma radiation (a human withstands 4 - 10 grays), temperatures ranging from 151 °C to near absolute zero −273 °C, and can live for 200 years.
- Recent studies have shown that only 82.5 % of the tardigrade's DNA is pure (see box on page 30), the remainder originating in plants, bacteria and fungi. These fragments of foreign DNA are incorporated during repairing processes of DNA damaged during exposure to hostile environments.



Light microscope images of tardigrades. (**a**) Ventral and (**b**) lateral view of their legs with claws. (**c**) Tardigrade exuvia (remains of the exoskeleton after the individual has moulted) containing eggs (dark circles). In many cases, the eggs are left inside the shed cuticle to develop. (DR, DL)

Taxonomy

Their scientific name Tardigrada was suggested by the Italian biologist Lazzaro Spallanzani in 1776 meaning 'slow walker'. A number of morphological and molecular studies have tried to resolve their systematic status, and recent analyses indicate that they are probably basal arthropods. The phylum Tardigrada includes three classes and over 110 genera, and is continuously updated with newly discovered species. For example, a new genus, *Pilatobius*, was proposed in 2014. The class Mesotardigrada includes only one species: *Thermozodium esakii*. This species was recorded in 1937 from a hot spring near Nagasaki, Japan. Unfortunately, this place was destroyed by an earthquake and subsequent searches for specimens have been unsuccessful.



Scanning electron microphotograph of (**a**) a tardigrade showing its typical plump shape (**b**) a tardigrade's retractile tubular mouth armed with stylets and used to pierce plant cells or the small invertebrates on which it feeds. (NC, JM, MJIB)

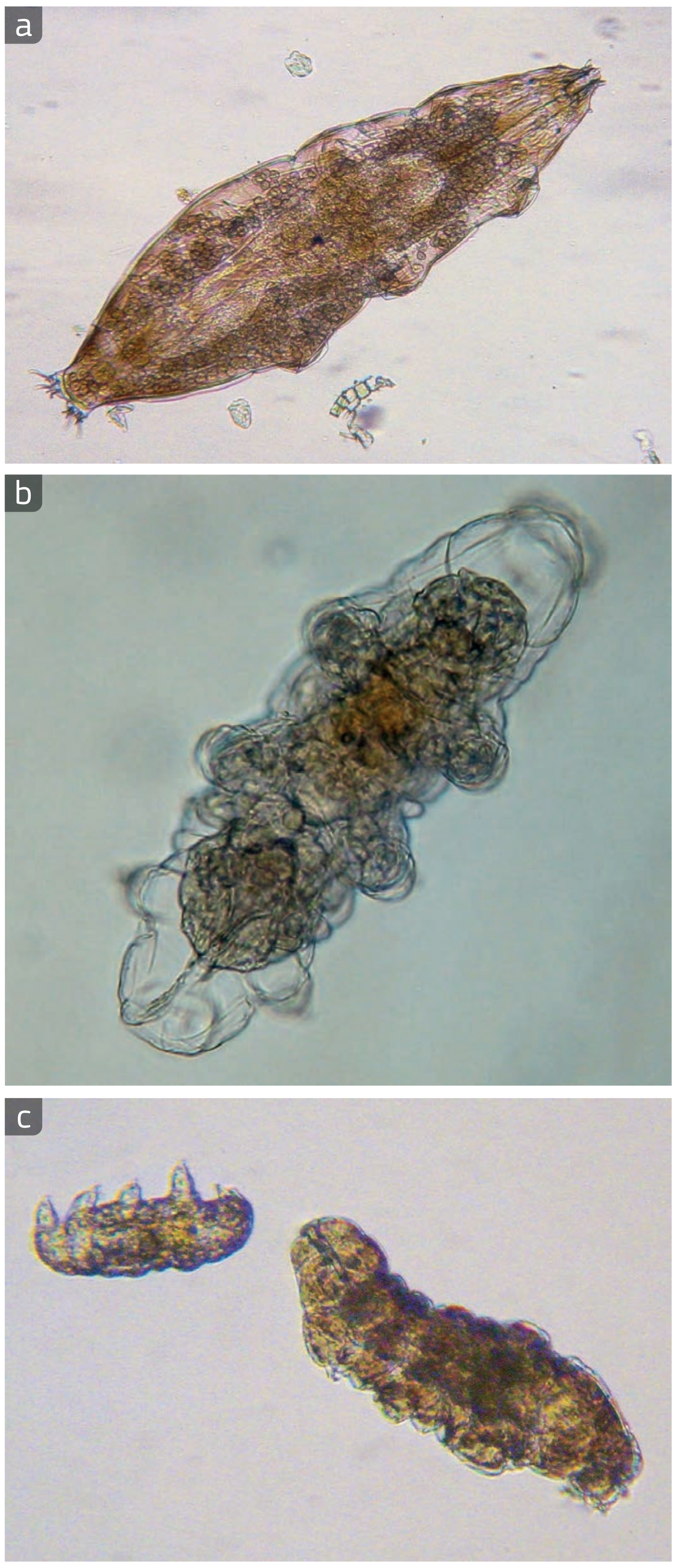
Tardigrades are also commonly known as 'moss piglets' as they are often found in mosses, where they eat plant cells or small invertebrates. (AO)

Microhabitat

Tardigrades are common in both marine and freshwater systems but also in the water films surrounding soil particles. They are also found in mosses, which are the plants that have the most developed capacity to absorb and retain water, thus giving them their second common name 'moss piglets'.

Diversity, abundance and biomass

Approximately 1 150 species of tardigrades have been described and can be found in almost every type of habitat around the world, from above 6 000 m in the Himalayas to the deep sea (below 4 000 m) and from the polar regions to the Equator. Many of these environments experience dramatic environmental changes throughout the year, and tardigrades survive thanks to their extraordinary ability to enter into 'cryptobiosis', a suspended animation (deathlike) state in which their metabolism drops to 0.01 % of normal (or is entirely undetectable) and the water content of the body decreases to less than 1 %. In this cryptobiotic state, known as a 'tun', they can live for a long time (up to 200 years!) and can survive extremes of temperature, toxicity, dehydration, salinity and oxygen tension. Revival typically takes a few hours but depends on how long the tardigrade has been in the cryobiotic state. Although their ecological role has not yet been fully evaluated, recent studies suggest they could have a regulatory function for plant-parasitic nematode populations when predatory nematodes have disappeared, due to predation pressure and/or unfavourable environmental conditions.

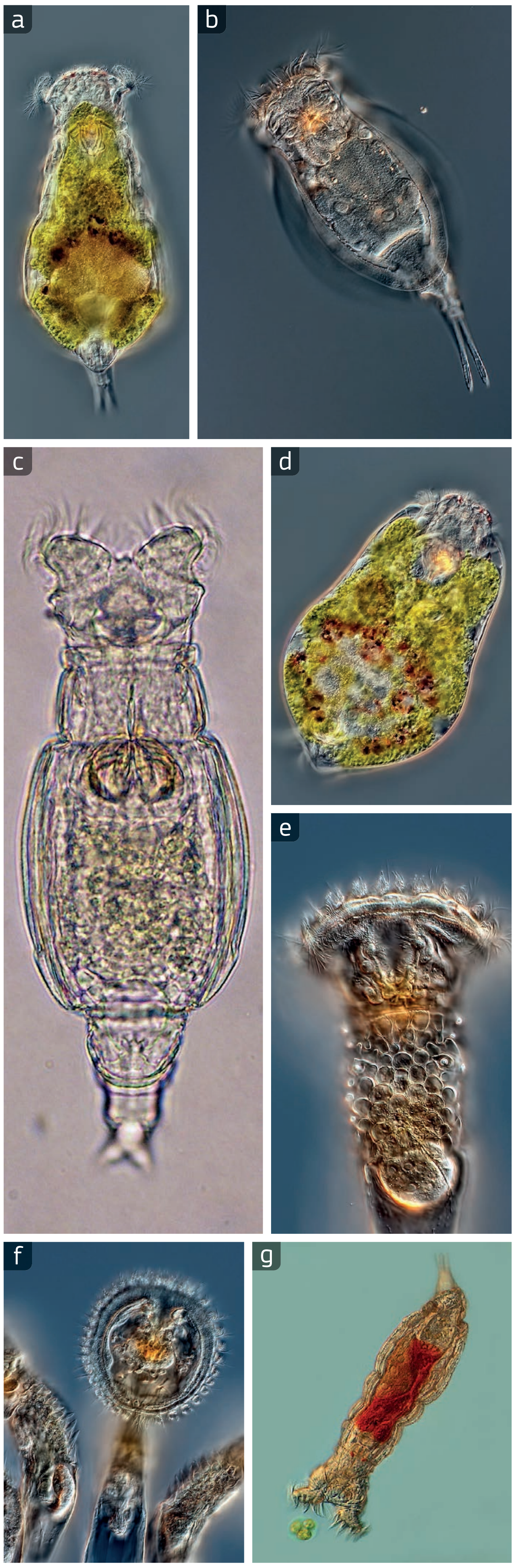


(**a**) Dorsal view of an adult specimen of *Milnesium* sp. with the head pointing to the right, where mouth parts and eye spots can be seen. On the left, back claws aid in identification. (**b**) Tardigrade as it recedes from its cuticle (outer covering) in preparation for moulting. In order to grow they must moult. (**c**) Female adult specimen and juvenile. (MS)

Microfauna – Rotifera

Morphology

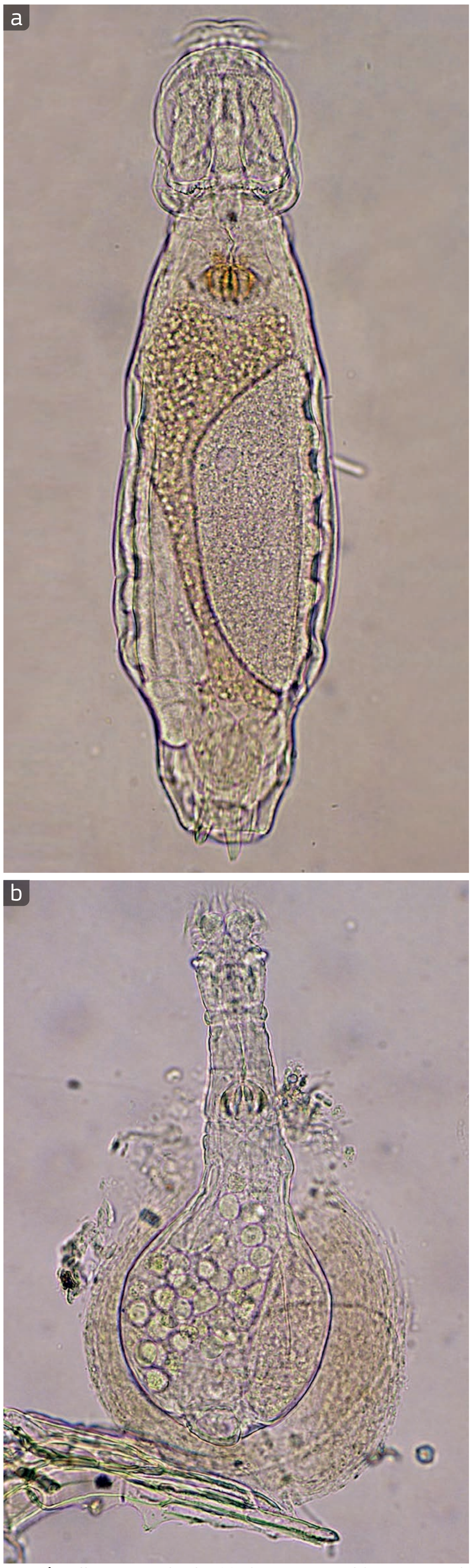
Rotifers are minute multicellular organisms (0.05 to 3 mm long). Their mostly transparent body is subdivided into a head, trunk, and a foot. They have three easily visible unique features: 1) their anterior ciliary organ called the corona (or crown); 2) a specialised food processing apparatus made of strong muscles and a set of hard jaws (the mastax with trophi); 3) a unique and well developed cuticle (the lorica), giving the animals a pseudo-segmented appearance, that can be exquisitely ornamented. The head and foot can be retracted inside the trunk if the animal is disturbed or if the environment dries out. [45, 46]



(**a–g**) Diversity of rotifers. *Philodina roseola* (**g**) has been used to study their ability to enter a slowed metabolic state in response to extreme environmental conditions, such as dessication. In this state, known as anhydrobiosis, development and reproduction are interrupted. They can remain in this state for several years and, when circumstances improve, they can revitalise in a few hours and continue with their normal activities. (RM, HS, PA)

Taxonomy

Rotifers (phylum Rotifera) are related to other worm-like organisms belonging to Gnathostomulida and Micrognathozoa. Recent studies in DNA evolution (molecular phylogeny) have revealed that the parasitic worms of the phylum Acanthocephala are their closest relatives, if not themselves a group of specialised rotifers. Scientists recognise three groups of Rotifera, but only one, the Bdelloidea, is an important soil inhabitant.



Different species of rotifers: (**a**) *Adineta* sp., species of this group are used as a model to study rotifers in the laboratory; (**b**) *Habrotrocha* sp.; species of this group have been found in leaf litter, soil and moss in Europe, New Zealand and North America. (HS)

Microhabitat

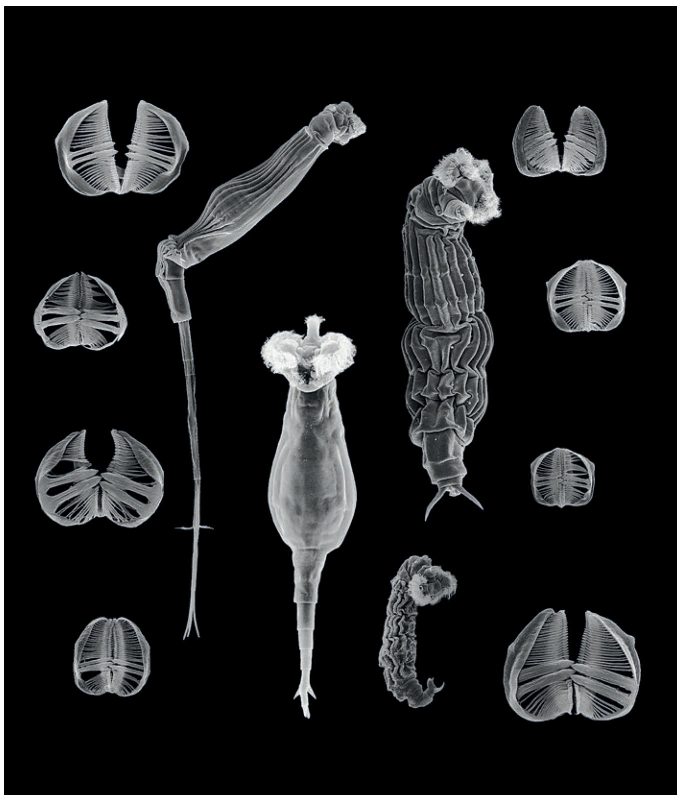
Like many other minute organisms, rotifers have an absolute requirement for a water matrix during their active phase. They inhabit the capillary water retained between soil particles, litter or mosses, where they feed on bacteria or small algal cells. They are filter-feeders (i.e. feed by filtering food particles from water) or browse the bacterium film for particles. A few are predators of ciliates or of other rotifers, or suck out the content of cells after piercing the cell wall using specialised trophi. Although they need water to live actively, the bdelloids, which are the most successful soil rotifers, have an extraordinary ability to survive prolonged periods of desiccation through a process called anhydrobiosis (a type of cryptobiosis – see page 44). In this state (known as a 'tun'), they not only survive adverse conditions but can also be easily transported to other habitats. Because of this and their reproductive features (see box, below) they are very effective at colonising and recolonising areas. Most rotifers, in particular bdelloids, can only be identified while alive. This has hampered their study significantly, to the extent that little is known of their role in the functioning of soil systems.

Bdelloid rotifers, a female affair

- Rotifers are usually dioecious (have distinct male and female organisms) and sexually dimorphic (have distinct male and female forms), with the females always being larger than the males. They reproduce sexually or parthenogenetically.
- Among rotifers, there is a particular group, the bdelloid rotifers, that originated around 80 million years ago, and there are now about 460 morphologically distinct species.
- Bdelloid rotifers have evolved entirely without sexual reproduction and are assumed to have reproduced without sex for many millions of years. Males are absent and females reproduce only by parthenogenesis.
- No male sex organs have ever been observed in these microscopic animals. Asexual reproduction is generally thought to be an evolutionary dead end as it leads to reduced diversity and the build-up of deleterious mutations.
- The ability to acquire new functions (i.e. of evolving) has been achieved by incorporating DNA fragments of other organisms, such as bacteria, algae and fungi into their genome. This process is known as horizontal gene transfer.
- These findings overturn current thinking that reproduction without sex is less likely to endure evolutionary changes than sexual reproduction.

Diversity, abundance and biomass

There are about 2 030 described species. They can be extremely abundant in moist soils and mosses but can occur in dry soils as well. They live in virtually every terrestrial habitat, from the Poles to the Equator, mostly near the soil surface.

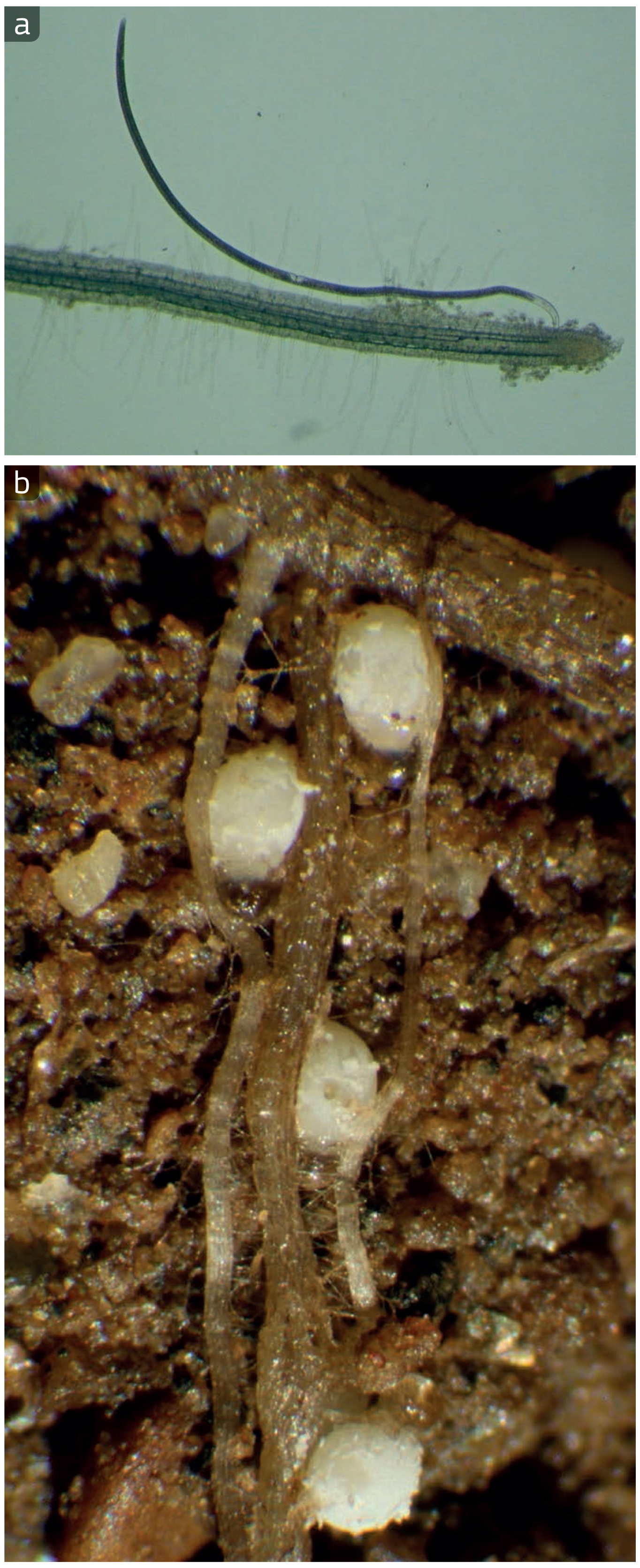


Scanning electron micrographs of morphological variation of jaws (trophi) and four different species belonging to the genus *Rotaria* (in the middle). The shape of the trophi varies between different species, depending partly on the nature of their diet. (DF)

Microfauna – Nematoda

Morphology

Nematodes are aquatic transparent roundworms (0.1 - 5 mm in length in soil species) and are dependent on water films surrounding soil particles for their activity and gas exchange. The ability of nematodes to have many food sources and to live in numerous habitats (marine and freshwater sediments, as parasites of plants, invertebrates and vertebrates) is due largely to their morphological adaptations and survival strategies. Nematodes survive the harshest conditions (desiccation, heat, freezing, osmotic and oxygen stress), by shutting down their metabolism, altering their biochemical pathways and body shape and entering a dormancy state (cryptobiosis – see pages 44 and 86), which is reversible when favourable environmental conditions return. While in cryptobiosis, they can be dispersed by wind. Nematodes generally have an elongated body shape tapering at both ends, but they also can be spherical or pear shaped. They have a non-segmented flexible cuticle and their body organs (excretory, nervous, digestive and reproductive systems) are in a fluid-filled cavity, called coelom, and present in many other animals (e.g. earthworms – see page 58). Their movement is undulatory, contracting certain muscles against internal pressure. Most soil nematodes have separate sexes but some can be parthenogenic or hermaphroditic. Nematodes generally lay eggs that develop through four moulting juvenile stages to adults. [47, 48]



Nematodes generally have an elongated body shape, but they also can be spherical or pear shaped. (**a**) The plant parasitic nematode, *Belonolaimus longicaudatus*, feeding on a plant root shows the typical lengthened shape. (**b**) Spherical females (white) of *Heterodera schachtii* feeding on a plant root. The eggs are laid inside the female body. (OB, JGB)

Taxonomy

The phylum Nematoda contains multicellular animals that are related to other moulting animals (the Ecdysozoa) such as Nematophora. Terrestrial nematodes predominate in the large orders of Panagrolaimida, Rhabditida, Mononchida and Dorylaimida.

Microhabitat

Global studies of the distribution of soil nematode species show that most are endemic to a site or region, and only a small fraction are cosmopolitan. Climate, vegetation, as well as soil physical and chemical characteristics all contribute to determining the habitat suitability of each community of nematode species. Nematodes are a key group for regulating biogeochemical cycling and ecosystem processes. These processes include mineralisation and decomposition in the soil system. Nematodes are also indicators of environmental quality. For these studies, nematodes can be differentiated into feeding groups based on their morphology and, in particular, the shape and size of their mouthparts. There are five main feeding types: bacterivores, fungivores, omnivores, plant parasites and predators. Ecological characteristics or life history traits of nematodes can also be indicators of environmental quality. For example, species that reproduce quickly in response to a nutrient-rich addition to the soil, are 'colonisers', while species with long life cycles and low reproduction rates are 'persisters'. Soil nematodes carry bacteria on their cuticle and can excrete viable bacteria, thus serving as a vehicle for translocation of bacteria throughout the soil, and as a potential food source.

Diversity, abundance and biomass

Nematodes are among the most diverse and abundant animals on Earth: one in five animals on Earth is estimated to be a nematode. Terrestrial nematodes make up a substantial portion of the more than 25 000 described species of the group. Nematodes are found in soils, marine and freshwater sediments, and as parasites of plants and animals, such as insects, humans and birds. Many nematode infections cause serious human diseases in the developing world (e.g. Guinea worm and elephantiasis).

Nematodes, everywhere!

- Soil nematodes feeding on bacteria occur more than 3.6 km below the surface of the Earth – deeper than any known animal, and at a temperature of 48 °C.
- The smallest nematode, belonging to the genus *Micronema*, is 0.3 mm in size and lives between sediment particles.
- Nematodes were the first animal genome ever sequenced, and are thought to be the most genetically diverse of all animals.
- Based on DNA sequences, two nematode species can be as different as a tiger and a mouse.
- Nematodes can survive in space and are known to have survived the U.S. Columbia Space Shuttle crash.
- A nematode released to control the invasive species of Sirex woodwasp (*Sirex noctilio*) has saved the Australian forest industry an estimated US$80 M (approx. €75 M) per year.
- In 2013, groundsmen at Scotland's national rubgy stadium sprayed a solution of garlic on to the field in a bid to cure a nematode infestation that was destroying the playing surface.

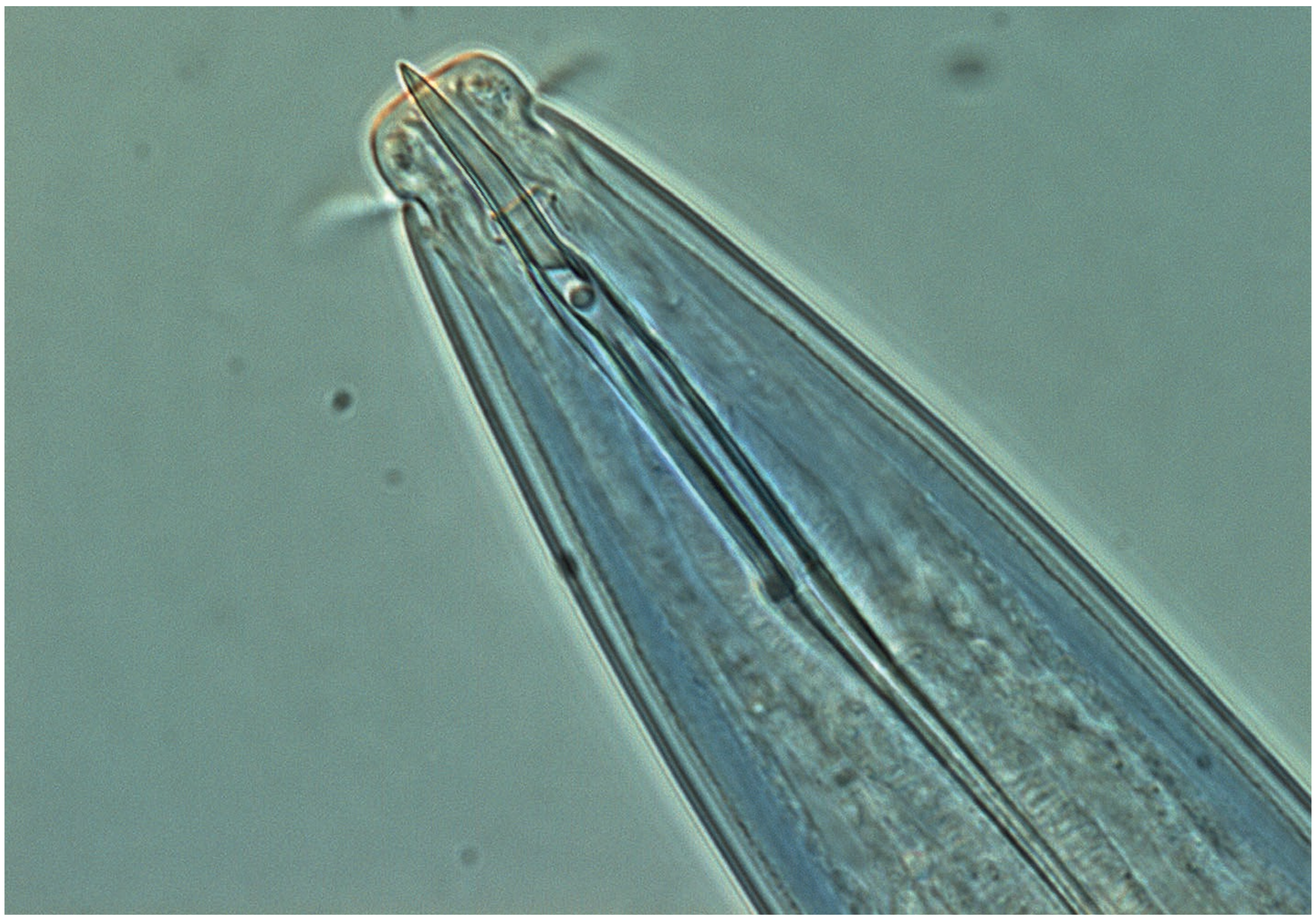
Plant-feeding nematodes

Nematodes puncture the cell walls of plant roots with large hollow needle-like spears in their mouths and suck out plant nutrients. Their spears are called stylets and vary in shape. Enzymes, (e.g. cellulase and chitinase) are injected through the stylets of some plant parasitic species to help break down cell walls. Other species, such as *Xiphenema* spp., can carry plant viruses in their stylets and vector the viruses from plant to plant. Plant-feeding nematode species can be migratory or sedentary, feeding either inside the host plant root (endoparasites) or outside the plant root (ectoparasites) and can cause serious economic damage to agricultural crops, including citrus, rice, maize, soybean and numerous vegetable crops. The plant parasitic nematodes *Meloidogyne* and *Pratylenchus* spp. infect wide ranges of host plants, while *Globodera* and *Heterodera* spp. have more restricted plant host ranges. Crop rotations help avoid damage by the latter two nematode species.

Plant-feeding nematodes. (**a**) Head of *Globodera pallida* with an extendable spear used to penetrate roots of host plant species, such as potatoes (*Solanum tuberosum*). Note the knobs on the base of the spear that anchor muscles extending forward to the head. When these muscles contract, the spear juts forward. (**b**) The plant hosts of the nematode *Helicotylenchus pseudorobustus* include: fruit crops, vegetables, agronomic crops, ornamental plants, forages, turfgrasses, weeds. (**c**) Grasses [e.g. *Elymus farctus* (Viv.)] are a host to this plant parasitic nematode species, *Meloidogyne duytsi*. (HM, HH, JGB)

Omnivorous nematodes

These are large free-living soil nematodes (up to 5 mm in length), and are omnivorous, using a variety of food sources. They have a hollow tooth that can pierce other organisms and suck out nutrients. Depending on environmental conditions and food availability, they can feed on algal filaments, protists, other nematodes and then, when their primary food sources are unavailable, switch to feeding on fungal hyphae and bacteria. They often have low reproduction rates and generally occur in stable habitats, rather than in newly established or disturbed habitats.



The omnivorous nematode *Prodorylaimus filarum* has a spear without knobs. Omnivorous species can feed on algae, protists, other nematodes and then, when these primary food sources are unavailable, switch to feeding on fungi and bacteria. (HM, HH, JGB)

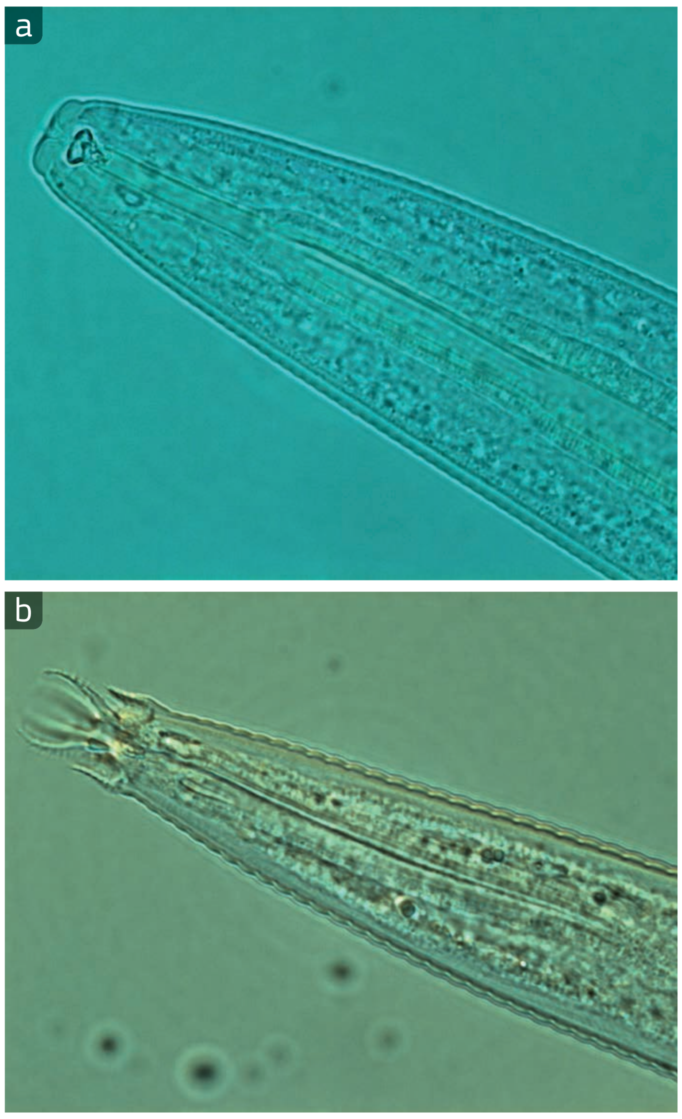
Predaceous nematodes

Predaceous nematodes have one or more large teeth or a pointed spear that are used to attack and ingest nematodes and other small animals, such as enchytraeids, tardigrades, rotifers and protists (see pages 36-37, 44-45, 48). Predatory nematodes make up approximately 5 % of the overall soil nematode community, and decline in abundance when soils are disturbed. *Mononchoides* spp. can also feed on bacterial cells and can be cultured in the laboratory as biocontrol agents against plant parasitic and other nematodes.

(**a**) This predator with a large dorsal tooth (*Mylonchulus sigmaturus*) eats other nematodes. (**b**) This predaceous nematode has a hollow spear to kill enchytraeids and other small animals. (HM, HH, JGB)

Bacterial-feeding nematodes

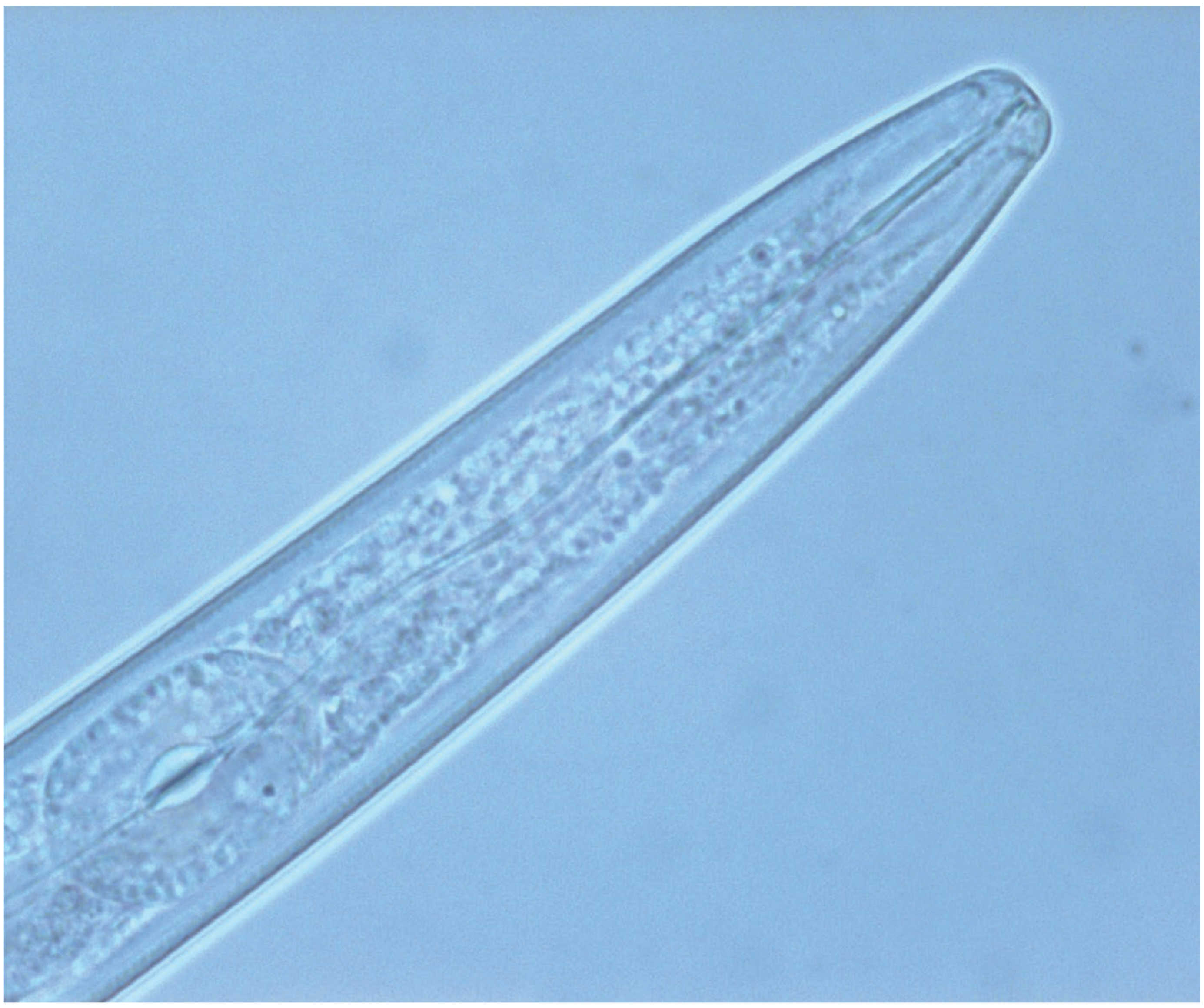
Bactivorous nematodes have tubular mouths and graze on bacteria by swallowing them or scraping them from soil substrates using structures on top of their head. Grazing of bacteria increases the rate of decomposition of the chemical compounds in organic matter (carbon and nitrogen mineralisation) in soil. There is also evidence that grazing on bacteria can positively affect the plant root growth. These animals have germination times ranging from a few days to a week, which is advantageous for colonising new habitats.



Bacterial-feeding nematodes. (**a**) *Anaplectus* has a muscular tubular mouth for engulfing bacteria and no spear. (**b**) *Acrobeles mariannae* has ornate head appendages (probolae). (HM, HH, JGB)

Fungal-feeding nematodes

Fungal-feeding nematodes have small, fine stylets optimally adapted for feeding on fungal hyphae (see box, page 39). Fungivorous nematodes can affect plant growth indirectly via the destruction of arbuscular mycorrhizal fungi (see page 40) or other beneficial fungi, leading to reduced nutrient availability for the plant. Other species are beneficial for pest control through the destruction of plant fungal pathogens (see box, page 39). Fungal-feeding nematodes are generally less abundant in highly disturbed soils (e.g. agriculture) than bacterial-feeding nematodes.



Fungal-feeding nematodes, such as *Aphelenchus* sp., have a tiny spear to pierce fungal hyphae. (HM, HH, JGB)

Mesofauna – Enchytraeidae

Morphology

Enchytraeidae are also known as ‘potworms’ and owe their name to first being discovered in flower pots (from the Greek *enchytraeon* meaning ‘in the pot’). Each body segment bears four bundles of bristles (setae), two located on the ventral side and two occupying lateral or dorsolateral positions. Numbers of setae per bundle vary between 1 and 16. However, two, three or four are most common, although in some species they are totally absent. Setae are resistent structures, made of chitin, that allow the animal to anchor itself to substrate. Like earthworms (see page 58) and leeches, they are hermaphrodites, as they have reproductive organs normally associated with both male and female sexes. They develop a ‘clitellum’, a glandular modification of the epidermis (the sheet of cells that covers the body of all animals) which secretes a cocoon where the eggs are deposited; however, some species can reproduce through parthenogenesis or asexually by fragmentation (see the box on the right). [49, 50]

An enchytraeid belonging to the species *Cernosvitoviella atrata* from the UK. This species was described for the first time in 1903. A scanning electron microphotograph shows the morphology of enchytraeids. They show annular segmentation and have bundles of bristles, called setae, used to anchor themselves to the soil. (NC, JM, MJIB)

Taxonomy

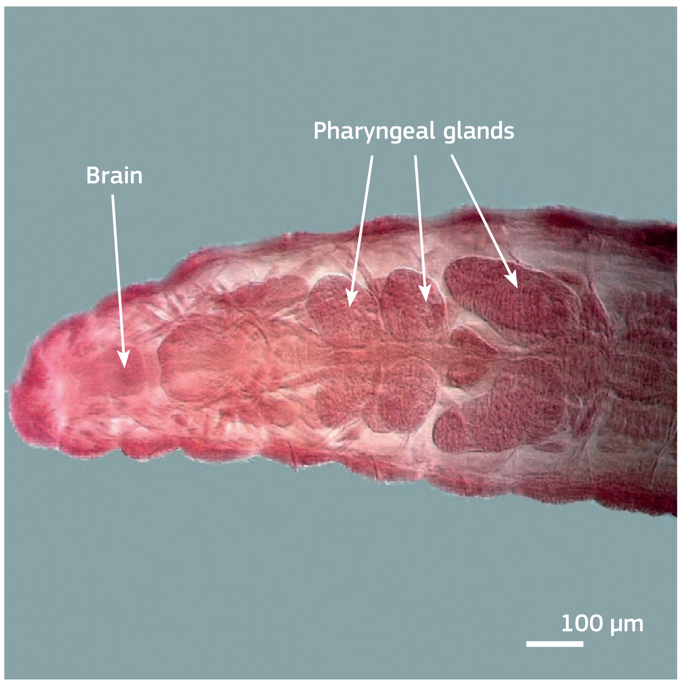
The Enchytraeidae are a family of Annelida (class Oligochaeta), resembling small white earthworms (1 - 30 mm in length) that include both terrestrial and aquatic species. Enchytraeids are identified when alive, since the taxonomy uses external and internal structures, which can be clearly seen only through the living transparent body. A single sample generally contains about 1 - 15 (rarely more) species. New species are often found; most subtropical and tropical species are still undescribed.

Microhabitat

Enchytraeids are concentrated in the uppermost soil layers (0 - 5 cm), where organic matter accumulates. Most studies regard them as microbial-feeders, frequently grazing on bacteria and fungal mycelia (see box, page 39), although they are also saprovores, consuming dead organic matter.

Diversity, abundance and biomass

About 700 valid species of enchytraeids have been described. Although they are distributed globally, they are more abundant in non-wooded habitats. In particular, cold and wet organic-rich environments, such as moorlands, contain high numbers (ranging from 12 000 to 311 000 individuals per m^2), and here enchytraeids are the dominant soil fauna (in terms of live biomass). Seasonal climatic fluctuations have a strong influence on their population dynamics, and extreme weather conditions, such as summer droughts and severely cold winters, can lead to high mortality rates. Although some species can migrate to deeper soil layers to avoid these adverse environmental conditions, this seems to be a short-term survival strategy due to a lack of food in these more humified horizons. Feeding and burrowing activities influence soil structure and turnover of soil organic matter, thus making them ‘ecosystem engineers’, like termites, ants and earthworms (see pages 54-55, 58).



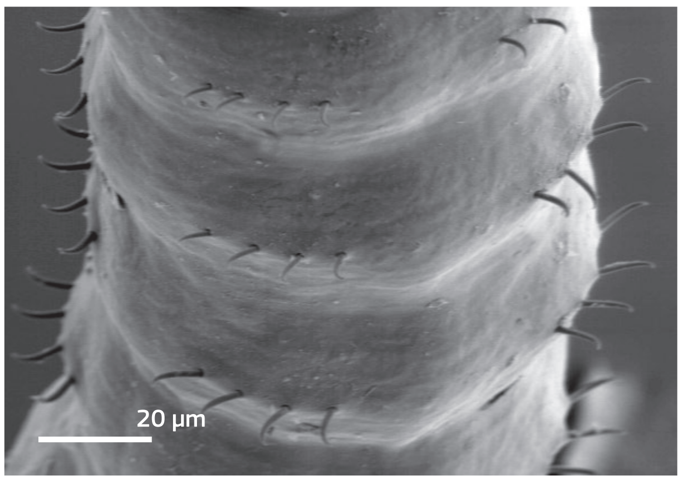
An enchytraeid belonging to the species *Bryodrilus ehlersi* from Hungary. Some internal structures, such as the pharyngeal glands and the brain, can be clearly recognised in this image. The pharyngeal glands are laterally paired in each segment in which they are present. They probably serve as a combination of digestive and lubricative functions. (KDF)

(**a**) An enchytraeid belonging to the species *Enchtraeus albidus* from a laboratory culture. Only some enchytraeids can be raised in the laboratory. To be identified enchytraeids need to be alive, since taxonomists rely on their external and internal structures, which can be clearly seen only through (**b**) the living transparent body. (RSC, AM)

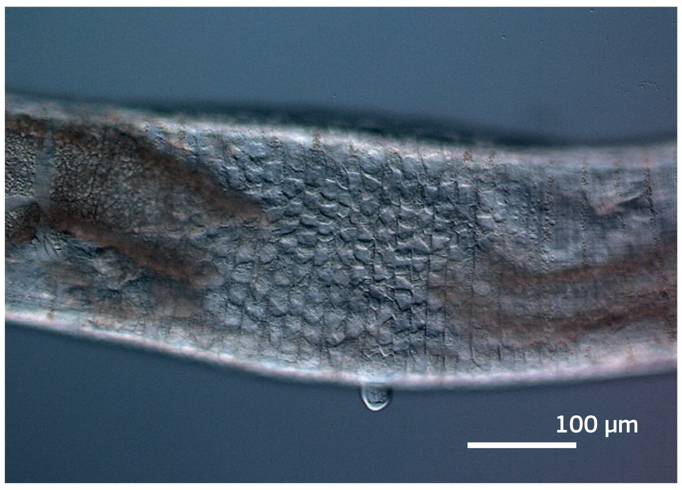
Nothing amazing, apparently...

- The most amazing fact about enchytraeids is that there is nothing amazing about them. However, it seems that cold, wet and organic rich ecosystems cannot function without them.
- The largest species (*Mesenchytraeus antaeus*) can be up to 6 cm long with more than 100 segments; the smallest species (*Marionina eleonorae*) is only 1 mm long and has no more than 15 segments.
- Enchytraeids have a variety of ways to reproduce: by ordinary cross-breeding, with both partners exchanging sperm and laying eggs; by self-fertilisation; by parthenogenesis (i.e. without fertilisation); and also completely asexually by breaking up of a worm into several pieces and regeneration of full-grown worms out of each piece.

Anterior end of the enchytraeid *Cernosvitoviella atrata* with a clear view of the first body segment, scientifically called prostomium, and the mouth. (NC, JM, MJIB)



Detail on the bundles of bristles, scientifically called setae, of the enchytraeid *Cernosvitoviella atrata* showing its characteristic sigmoid shape. (NC, JM, MJIB)



Lateral view of the clitellum of the enchytraeid *Marionina vesiculata*. The clitellum is a glandular modification of the epidermis that secretes a cocoon in which the eggs are deposited. (KDF)

Mesofauna – Acari

Morphology

Soil mites are relatively small (from 60 μm to 2-5 mm), have rounded or elongated bodies and, like other Arthropoda, are covered in a rigid structure, called exoskeleton or cuticle. Adult mites and nymphs have usually four pairs of legs, while larval stages have three pairs. They lack jaws and use the chelicerae and pedipalps (cephalic appendages) to grab their food. Chelicerae are diverse in form, which reflects mites' varied feeding habits. Most are ground-dwelling (i.e. subterranean) and some have one or two pairs of simple eyes (ocelli) in their outer covering. Being blind, they generally rely on physical and chemical sensing during navigation through the small soil pores. [51, 52]

Taxonomy

Mites (Acari) are an ancient lineage that have been known since the Devonian period, at least. Traditionally, they belong to the class Arachnida, together with spiders. There are roughly 40000 described soil-living species and more than half of them live on or in the ground. Representatives of both mite superorders (Acariformes and Parasitiformes) are found in soils. Moreover, they comprise up to 40 % of all soil microarthropod species.

Microhabitat

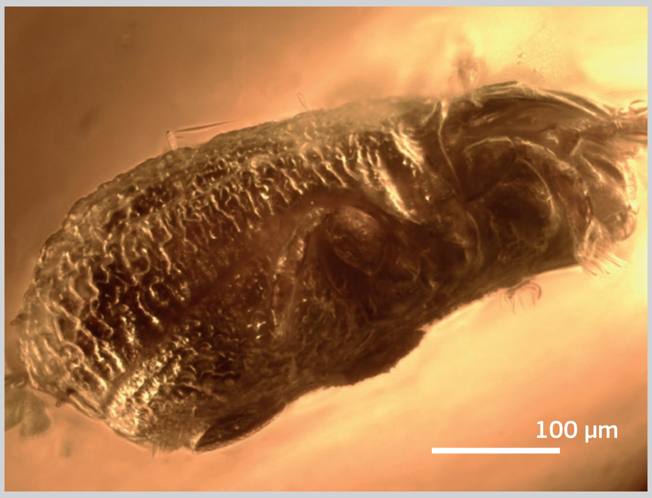
Soil mites occupy practically all natural soil substrates and have a world-wide distribution. They spread across all soil horizons starting from the surface of the litter down to 2-3 m in mineral soil. Their normal abundance in undisturbed ecosystems varies from a few hundred individuals in the arctic and tropical deserts up to one million per square metre in temperate mixed forests. Mites are among the first animals to colonise emerging mineral and organic substrates. They disperse in various ways, allowing them to cover large distances. These methods include: transport on mammals, birds and insects (phoresy), as well as passive distribution by wind or flowing water. Most mite species are characterised by clearly defined feeding habits, and their contribution to the cycles of carbon and nitrogen (see pages 104-105) in soil is fairly well quantified. Acariform mites have a variety of feeding preferences, from microbes (microbivory) and the remains of plants and animals (detritophagy) through omnivory to predation. Parasitiform mites are predominantly predaceous as they survive by preying on other organisms.

Distribution, abundance and biomass

In undisturbed systems, hundreds of mite species can be found in one square metre of soil. However, little is still known about general distribution patterns of mite species globally. Despite numerous reviews at both regional and global geographic coverage levels, the drivers of most general trends in mite species richness are not completely understood. However, they seem to be related to climate, availability and quality of organic matter, intensity of disturbance and the geological history of individual regions. Latitudinal climatic gradients are expected to be the major factor explaining regional oribatid family and species richness across large areas.

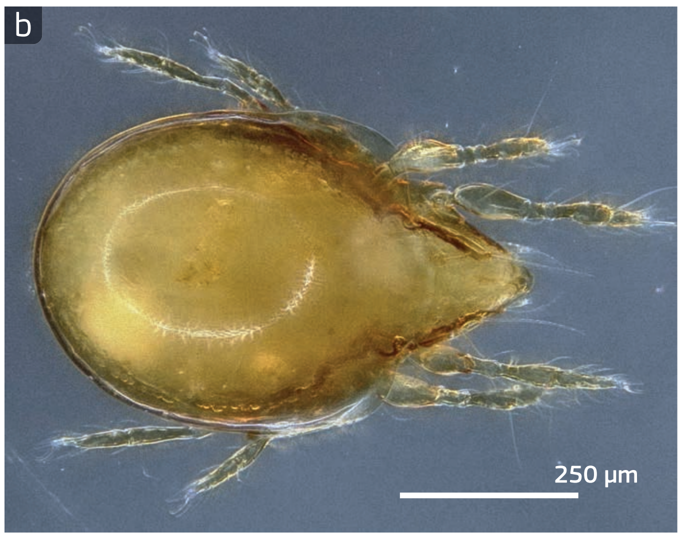
An exceptional persistence in nature

- Mites can withstand doses of radioactivity 100 times higher than those that would kill a human being.
- In heavily disturbed ecosystems, such as cities or industrial areas, soil mites can be the last indicator of primary habitats (i.e. habitats present before the development of cities/factories).
- This means that it is still possible to reconstruct the vegetation type and landscape conditions based on the mite communities remaining in the degraded areas.
- Oribatid mites (belonging to the superorder Acariformes) have hard exoskeletons that often fossilise.
- That is why fossil mite assemblages, together with pollen analyses, are used by scientists as an additional tool for palaeogeographic (the study of past geography) reconstructions.



Scutoribates perornatus encapsulated in Baltic amber. This amber dates back 44 million years (during the Eocene). Complex microscopy techniques were used to identify this species. (ES)

Dissoloncha superbus (belonging to the superorder Parasitiformes) is a group of predator mites inhabiting coastal areas of northern countries. It belongs to the order Mesostigmata. (KM)



Examples of oribatid mites (belonging to superorder Acariformes). (**a**) The mite *Tectocepheus velatus* was described in 1880 and has a worldwide distribution. However, it is still under discussion as to whether this is actually a single highly variable species or a group of similar species. (**b**) *Scheloribates pallidulus* is very common in grassland soils in the Northern Hemisphere. (**c**) *Oribatella rossicus*, another 'winged' oribatid mite, can be found in the Far East. (AZA)

Two mite species belonging to the genus *Steganacarus*. (**a**) *Steganacarus phyllophorus* under unfavourable conditions can curl into a very rigid sphere protecting soft tissues and extremities from predators. These minute soil 'armadillos' may feed directly on plant debris while other oribatids are predominantly bacterial- and fungal-feeders; (**b**) a scanning electron microphotograph of *Steganacarus* sp. (AZA, SMNG)

Mesofauna – Collembola

Morphology

Collembola are small (0.12 - 17 mm) wingless hexapods (with six legs – see page 31) commonly known as 'springtails'. The scientific name, Collembola, derives from the Greek words *kolla* (meaning 'glue') and *embolon* (meaning 'piston') and was initially proposed in reference to the ventral tube (collophore), which plays an important role in their fluid and electrolyte balance and may also serve as a 'glue piston' for adhering to smooth surfaces or for grooming. Another characteristic, albeit not always present, gives them their common name: the forked springing organ or 'furca'. This is held by a special catch mechanism on the ventral side of their abdomen which, when released, acts as a spring that can propel them, within seconds, several times the length of their body. [53, 54]

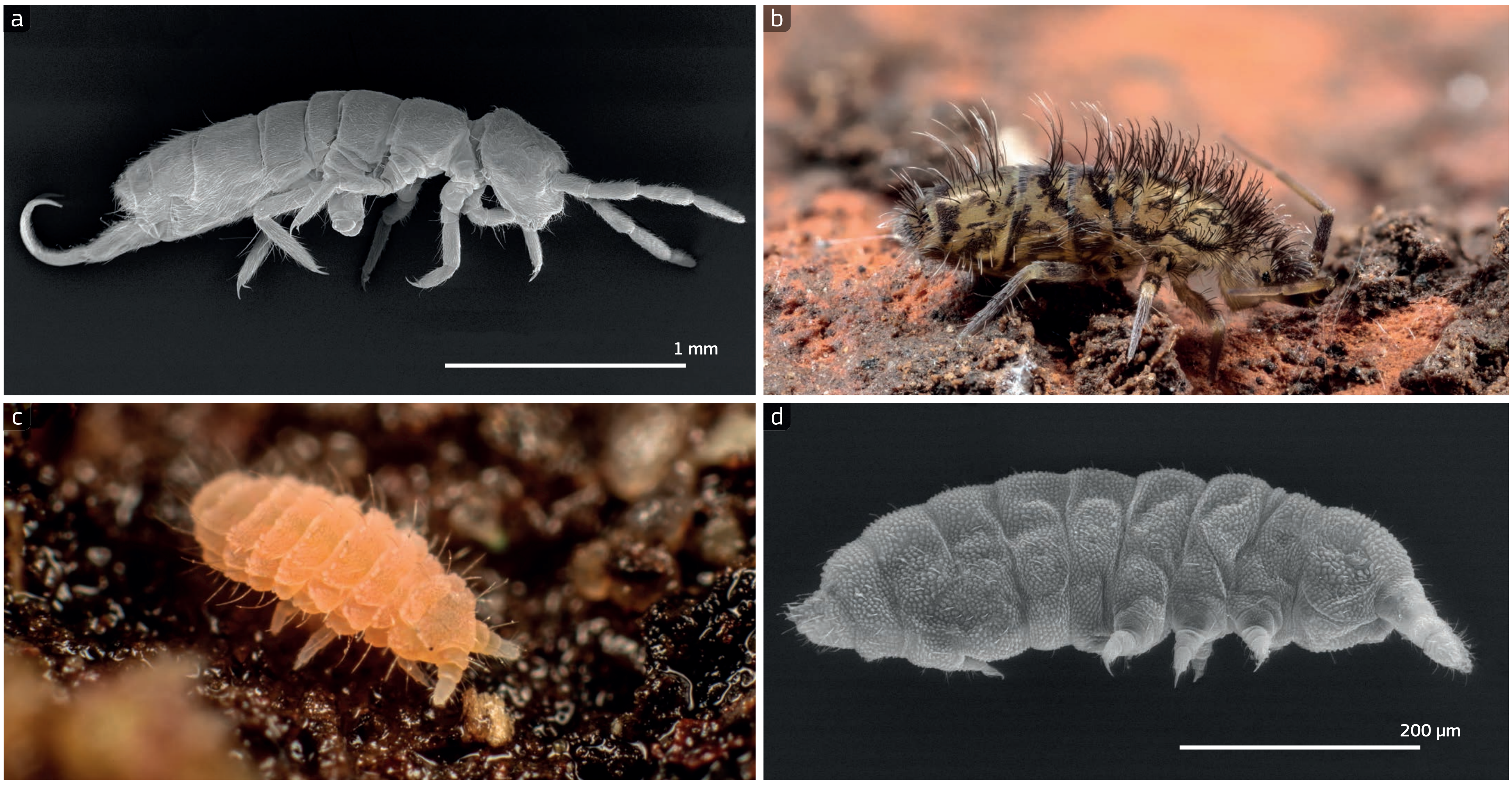
Microhabitat

Collembola vary in their habitat preferences. Entomobryomorpha and Symphypleona are mainly epiedaphic, living in surface litter and emergent vegetation, and are fast movers and good jumpers, whereas the slow-moving Poduromorpha and Neelipleona are mainly within-soil dwellers (euedaphic). Most Collembola feed on fungal hyphae and spores (see box, page 39), bacteria (see pages 33-35) and decaying plant material. However, ssome species are predators, feeding on nematodes (see pages 46-47) or on other Collembola and their eggs. Ecologically, they are not as important as earthworms in decomposition processes, but are still responsible for up to 30 % of total soil invertebrate respiration, depending on the habitat.

Diversity, abundance and biomass

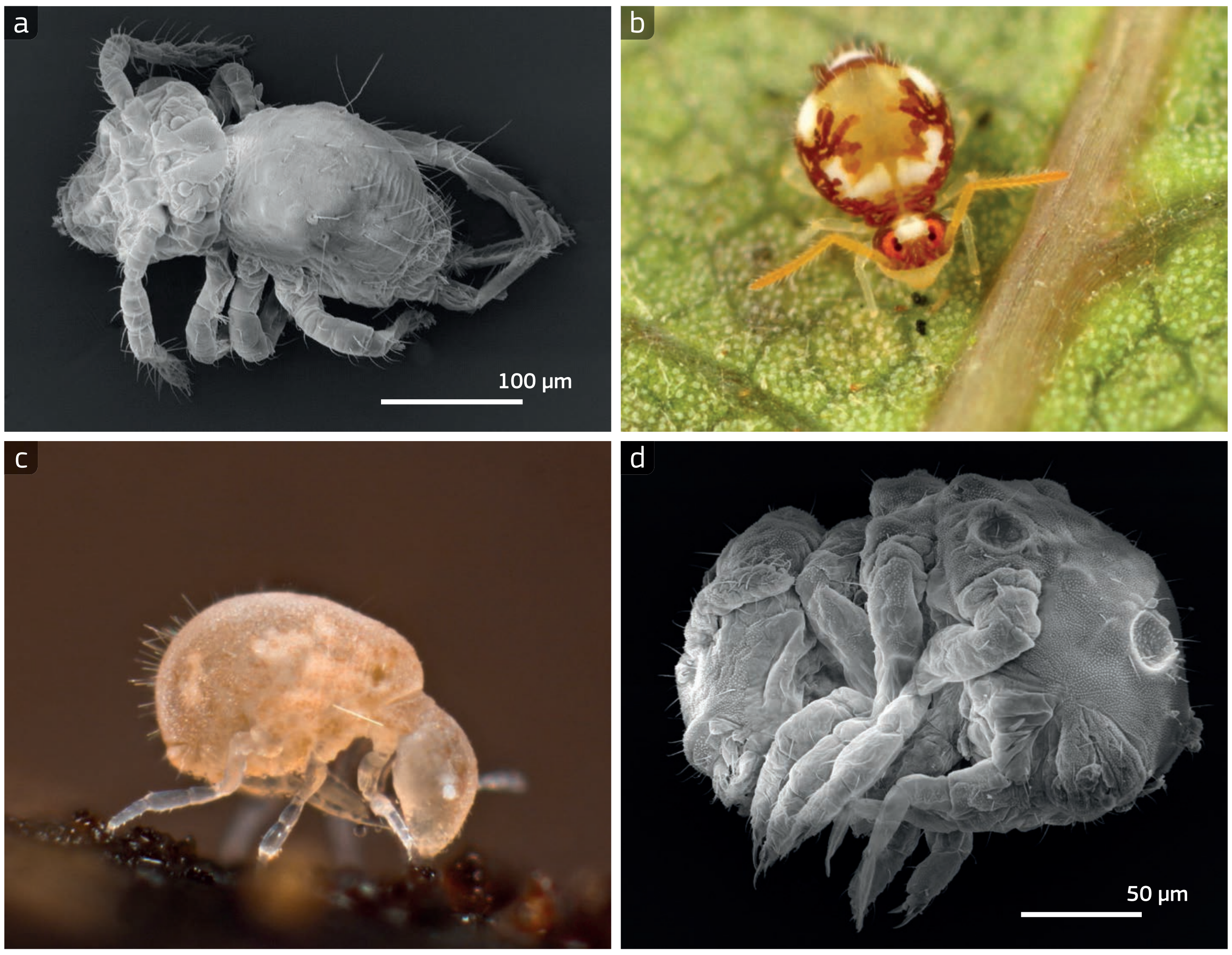
There are around 8 500 described species, which are found in a great variety of habitats, from Antarctica and the Subantarctic Islands to rainforests, warm beaches and deserts. As well as being widespread, they are the most abundant hexapods in the world, and an average square metre of soil in a temperate grassland or a woodland can yield as many as 40 000 individuals.

Generally, habitats may support anything from two to 30 different collembolan species. However, in the tropics, up to 150 species can be found, if species present in epiphytes (plants living in trees) are taken into account.



Order Entomobryomorpha: (**a**) scanning electron microphotograph showing the elongated shape, the distinctive abdominal segmentation, the long antennae and the well-developed furca; (**b**) live specimen of *Orchesella villosa* from the UK. (AM, NC, JM, MJIB)

Order Poduromorpha: (**c**) live specimen of *Monobella grassei* from the UK; (**d**) scanning electron microphotograph showing the elongated shape, the distinctive abdominal segmentation, the short antennae and the less well developed furca. (AM, NC, JM, MJIB)



Order Symphypleona: (**a**) scanning electron microphotograph showing the rounded body shape and the antennae as long as or longer than the head; (**b**) live specimen of *Katiannina macgillivrayi* from the USA. (NC, JM, SJS, MJIB)

Order Neelipleona: (**c**) live specimen of *Neelus murinus* from the UK; (**d**) scanning electron microphotograph showing the rounded body shape and the antennae that are shorter than the head. (AM, NC, JM, MJIB)

Taxonomy

Collembola belong to the phylum Arthropoda. They are part of the class Entognatha that, together with the class Insecta, form the subphylum Hexapoda (see page 31). They are classified into four orders: the Entomobryomorpha and Poduromorpha, with a more or less elongated body shape, and Symphypleona and Neelipleona, which are spherical in shape.

The frozen and colourful collembola

- Collembola can withstand freezing conditions by using anti-freeze compounds in their body tissues.
- *Cryptopygus antarcticus*, native to Antarctica and Australia, is the only Collembola species to have appeared on a postage stamp.
- Collembola can have multi-coloured stripes: *Paralobella orousetii* from the Philippines has a yellow head and first two thoracic segments, the third thorax segment and the first three abdominal segments are red and the remaining abdominal segments are white.

Mesofauna – Protura

Morphology

Proturans are small soil-inhabiting primitive hexapods (ranging in size from 0.5 and 2.5 mm – see page 31) with no antennae and no eyes. The forelegs are used as sensory organs; they have many sensory organs ('sensilla') covering their posterior segments (tarsi). On the dorsal side of the head there are a pair of other important sensory organs (pseudoculi) whose functions are not well understood. Their bodies are cylindrical, pointed at both ends and generally unpigmented, pale or yellowish. Similar to the Collembola, they are wingless arthropods and their mouthparts are entognathous, meaning that they are retracted within the head capsule: the mandibles and maxillae are slender and their maxillary palps (mouthparts) are long, with setae and sensilla. They are born with nine abdominal segments and grow by successive moultings during which they add new distal segments. The adult has 12 abdominal segments. They have small pairs of lateral-ventral appendages on the first three abdominal segments. They lack cerci, the paired appendages on the rear-most segment of the body present in many other hexapods. Reproduction occurs with indirect fertilisation: the males deposit packets of sperm (spermatophores) and the females collect the spermatophores. [55, 56]

Morphological structures of the proturan *Acerentomon italicum*: (**a**) the sensory organs, sensilla and setae, on the exterior side of the legs; (**b**) pseudoculi, the eye-like structures that are not actually eyes, on the dorsal side of the head; (**c**) the mouthparts are entognathous, meaning that they are retracted within the head. (LGA)

Taxonomy

The class Protura (phylum Arthropoda, subphylum Hexapoda) includes three orders: Acerentomata (families Hesperentomidae, Protentomidae and Acerentomidae), Sinentomata (families Fujientomide and Sinentomidae) and Eosentomata (families Eosentomidae and Antelientomidae).

The 'young' proturans

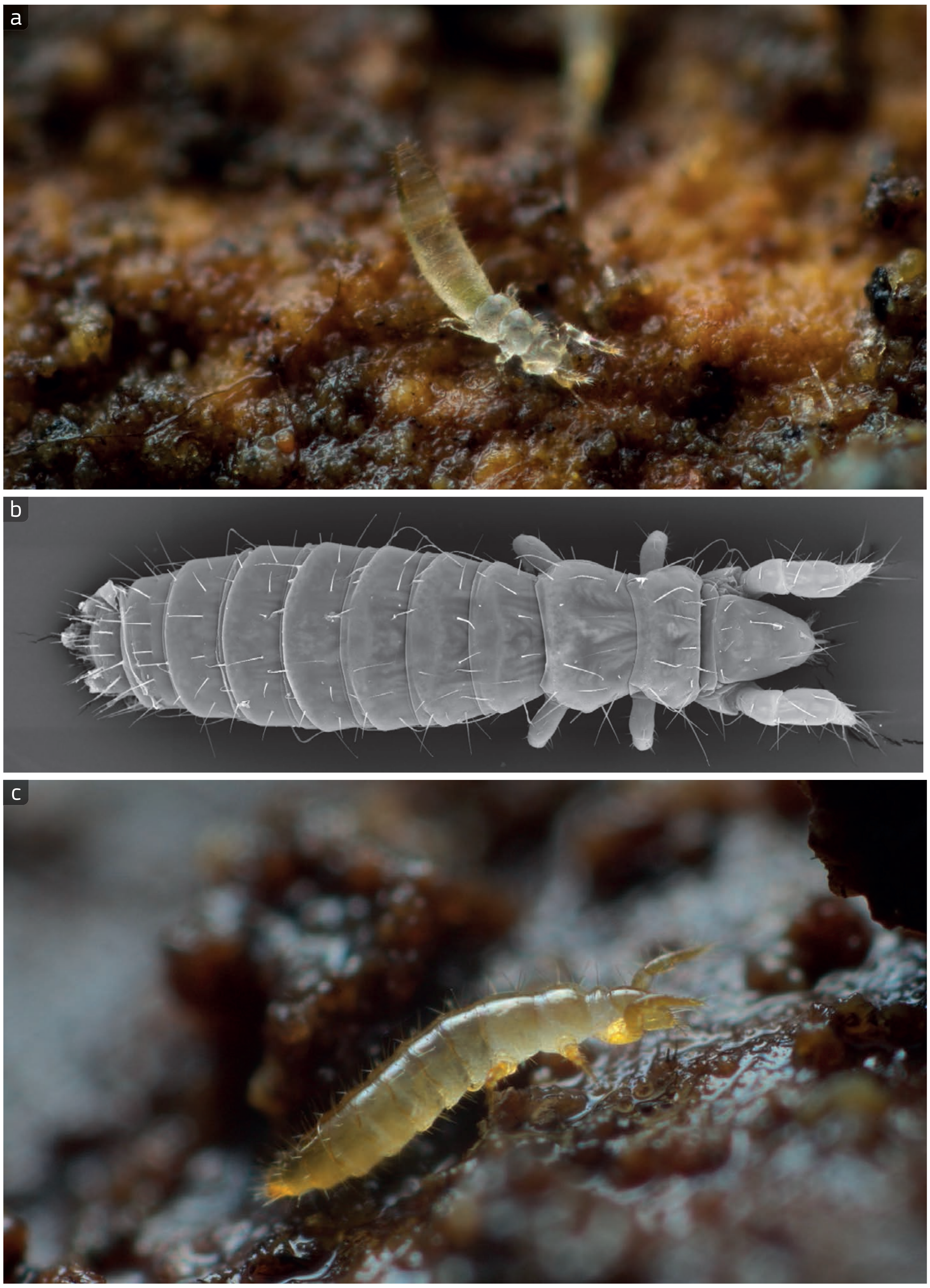
- Among hexapods (see page 31), Protura was the last class to be described. The first description of these minute soil arthropods was given in 1907.
- Filippo Silvestri and Antonio Berlese, two Italian entomologists, discovered proturans independently.
- The first species to be described was *Acerentomon doderoi,* found in soil near Syracuse, New York, USA.
- When disturbed, proturans seem to raise the end of the abdomen in a defensive posture similar to that adopted by scorpions.

Microhabitat

Protura are found in moist soils, leaf litter, humus, moss and decaying wood in woodland, grassland and agricultural soils. They do not thrive in very acid soils (e.g. coniferous woodlands). Usually, they are part of the decomposer community and help break down organic matter in soil and litter. In particular, proturans feed mainly on fungal hyphae (see box, page 39), but they are also important prey for small predators, such as spiders, mites (see page 49) and pseudoscorpions (see page 53).

Diversity, abundance and biomass

Proturans are found all over the world, with the exception of the polar regions. There are more than 700 described species. Their density is variable in relation to the characteristics of the soil and the content of organic matter. In disturbed and degraded soils they can be completely absent, while in undisturbed habitats, such as natural grasslands, there can be as many as 85 000 individuals per square metre.

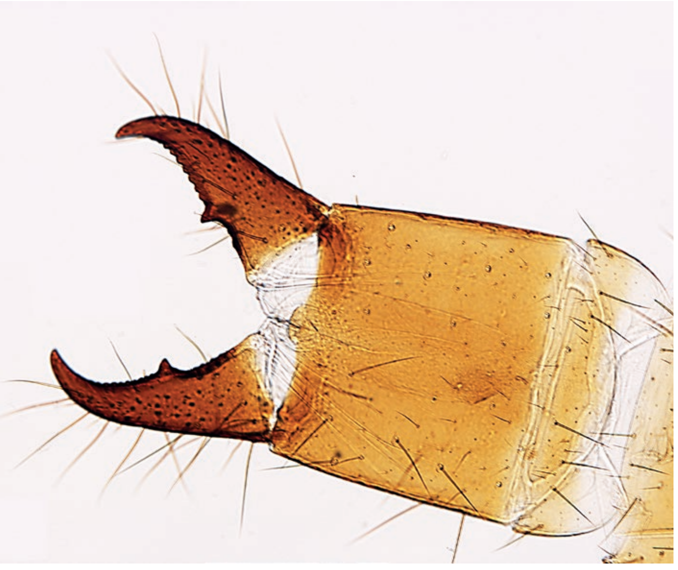


(**a**) and (**c**) Proturans in their natural environment in New Zealand and the UK, respectively. Proturans live mainly in soil, mosses and leaf litter in moist temperate forests. (**b**) Scanning electron microphotograph shows the dorsal part of the species *Acerentomon italicum.* (AM, LGA)

Mesofauna – Diplura

Morphology

Diplura are small wingless hexapods (see page 31), with body lengths ranging from 0.3 to 1 cm, although the largest species can be longer than 2 cm. Diplurans have a narrow and elongated body, and are generally white or colourless. The head has a pair of long and moniliform (a string formed of bead-like segments) antennae and no eyes. The abdomen ends with a pair of cerci, i.e. prominent abdominal appendages, which can contain silk glands. The cerci can have either a pair of pincers (Japygoidea) or can be filamentous (Campodeoidea). Some species of japygid Diplura are robust and darker in colour, and are often confused with earwigs (Dermaptera – see box to the right). However, Diplura have neither eyes nor wings. Fertilisation is similar to that found in proturans and collembolans (see pages 50-51): the males produce and deposit a large number of spermatophores, capsules containing spermatozoa, on the substrate that are then picked up by a female. The females lay eggs in clumps in the soil cavities or decomposing vegetation. Some species check the eggs and the larvae. Diplura are known to be able to regenerate lost body parts, such as legs, antennae and cerci. [57, 58]



Detail of the pincer-like stuctures of the dipluran *Catajapyx aquilonaris* belonging to the family of Japygidae. These abdominal appendages are scientifically known as cerci. (NS)

Taxonomy

The class Diplura (phylum Arthropoda, superclass Hexapoda) comprises nine extant families, the main ones being Japygidae and Campodeidae (each with more than 400 species).

Microhabitat

Diplura live in wood, leaf litter, under stones, rocks or logs, on the surface of, or in deeper layers of soil, in mosses or in termite and ant nests. Many species are herbivores and detritivores (feed on decomposing plant and animal parts) and feed on a wide range of plant material. However, some species have well-developed mandibles and eat nematodes (see pages 46-47), small arthropods, enchytraeids (see page 48), etc. They can also consume fungal mycelia (see box on page 39) and plant detritus. They are often part of the decomposer community, helping recycle dead plant material.

Diversity, abundance and biomass

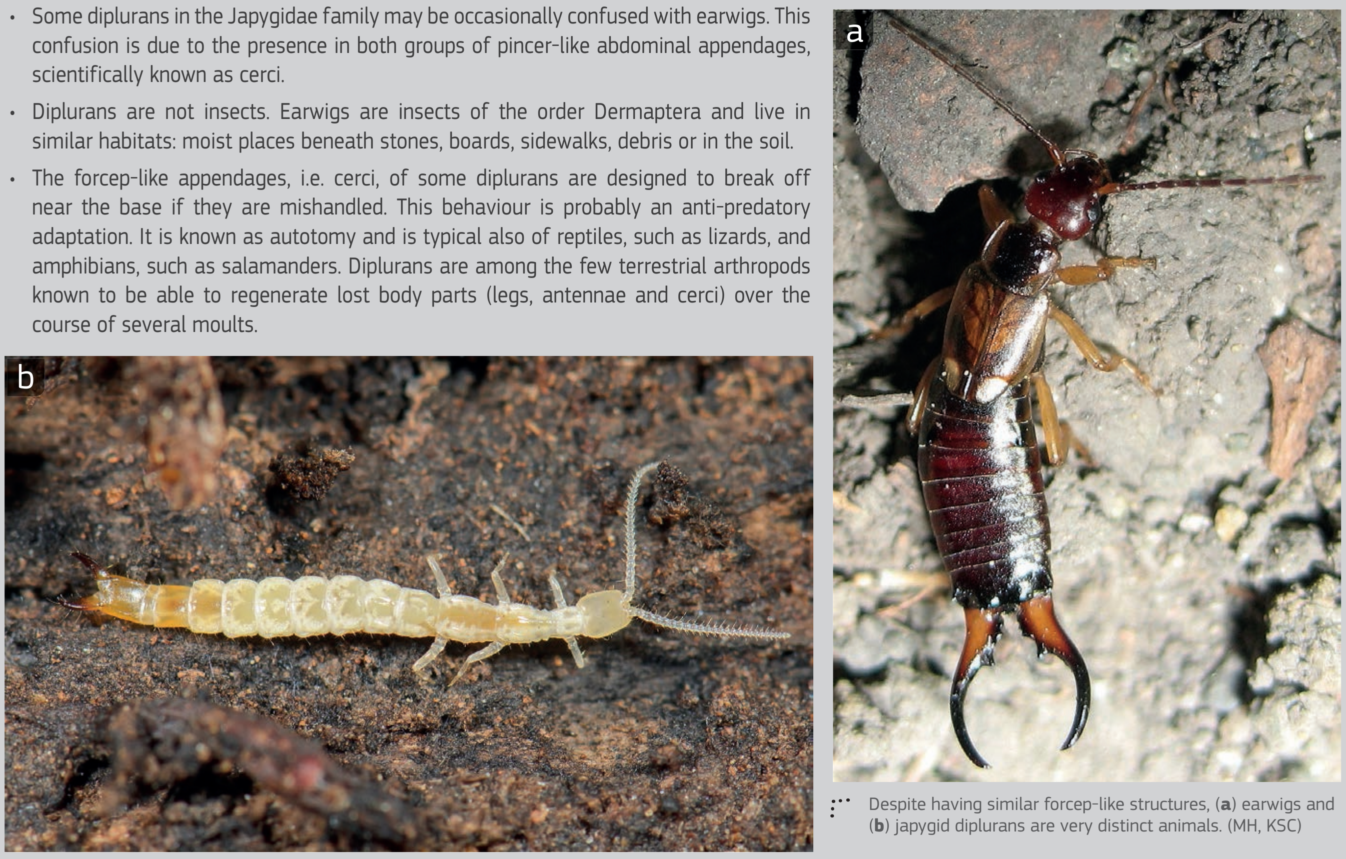
There are approximately 1 000 described species that are common inhabitants of most natural and human modified soils. They are distributed worldwide, from the tropics to temperate zones. They do not have specific habitat preferences and, generally, their population densities are not high (< 50 individuals per square metre).

Maternal care of diplura

- Male diplurans produce large numbers of spermatophores (up to 200 per week), probably because sperm only remain viable in the spermatophore for about two days.
- The eggs of campodeid and japygid diplurans are normally laid in a mass of up to 40, in clumps or on small stalks in little cracks or cavities in the ground.
- Female campodeid diplurans abandon their eggs, but japygid species are known to remain in the brood chamber with the egg cluster, protecting the eggs and the newborn larvae.

Diplurans are not earwigs

- Some diplurans in the Japygidae family may be occasionally confused with earwigs. This confusion is due to the presence in both groups of pincer-like abdominal appendages, scientifically known as cerci.
- Diplurans are not insects. Earwigs are insects of the order Dermaptera and live in similar habitats: moist places beneath stones, boards, sidewalks, debris or in the soil.
- The forcep-like appendages, i.e. cerci, of some diplurans are designed to break off near the base if they are mishandled. This behaviour is probably an anti-predatory adaptation. It is known as autotomy and is typical also of reptiles, such as lizards, and amphibians, such as salamanders. Diplurans are among the few terrestrial arthropods known to be able to regenerate lost body parts (legs, antennae and cerci) over the course of several moults.



Despite having similar forcep-like structures, (**a**) earwigs and (**b**) japygid diplurans are very distinct animals. (MH, KSC)

Campodeidae diplurans. (**a**) A live specimen shows the typical shape of this group. They are pale, eyeless hexapods and have two long abdominal appendages and antennae. (**b**) A live specimen of *Campodea augens* on moss. They can be found also in moist soil, wood, leaf litter and under stones. (AM, NS)

Mesofauna – Pseudoscorpionida

Morphology

Pseudoscorpions are tiny arachnids known as 'false scorpions' because they look similar to scorpions but do not have an elongated postabdomen with a venomous sting at the end. Usually less that 5 mm in length, they are brownish arachnids with large pincer-like chela (pedipalps). The body is divided in two regions: the cephalothorax (or prosoma, a fused head and thorax) and the abdomen (or opisthosoma) clearly divided into 11-12 segments. The cephalothorax is covered dorsally by a shield (carapace) and bears the appendages. One to two pairs of simple eyes (ocelli) are sometimes present on the head, but many species are blind. The first pair of cephalic appendages, the chelicerae, are two-segmented, chelate (clawed) and used for feeding. Chelicerae have silk glands. Behind the chelicerae are the pedipalps, which are used to capture prey and for defence. Pseudoscorpions, like all arachnids, have four pairs of thoracic legs. The abdomen has no appendages. These animals have a long lifecycle (the course of developmental changes through which an organism passes from its birth to the mature state in which it may give birth to another organism), depending on the environment and the temperature. The males produce a spermatophore, and pull the female over it. The female carries a silken egg bag of about 12-40 eggs in a brood sac that is attached to the ventral surface of the opisthosma. She can produce several broods each year. The young pseudoscorpions moult, passing from several larval instars (protonymph, deutonymph and tritonymph) before becoming adults that can live three to four years. [59]

Detail of the cephalic appendages of a pseudoscorpion. The smaller ones (dark red) are called chelicerae; the bigger ones (pale red) are the pedipalps and have a defensive function. (AM)

Female pseudoscorpion carries its brood sac. (MY)

Taxonomy

The Pseudoscorpionida or Pseudoscorpiones is a large group comprising 27 different families. They are found everywhere, but their highest diversity is found in the tropics.

A beetle for a house

- The dispersion of the tropical American pseudoscorpion *Cordylochernes scorpioides* from one tree to another is mediated by the Harlequin beetle *Acrocinus longimanus*. The males show territorial behaviour on the back of the beetles and even mate with females there.
- *Nesticus birsteini* (today *Carpathonesticus birsteini*) distributed in Russia and Georgia, is the only pseudoscorpion to have appeared on a postage stamp.

Microhabitat

Pseudoscorpions live under bark and stones, in leaf litter, in caves, under rocks on the ground and in soil. They are also often found in moss and lichens, in ant and bee nests and in the burrows of ground-dwelling mammals. The cosmopolitan species *Chelifer cancroides* is often found in houses.

Diversity, abundance and biomass

Approximately 3400 species of Pseudoscorpions have been described. Their density, in general, is not high (< 300 individuals per square metre). In some cases they are considered beneficial to humans as they prey on various pest species; for example, carpet beetle larvae, ants, mites and booklice. Occasionally Pseudoscorpiones may disperse attached to flying insects, birds and mammals (phoresy).

Diversity of pseudoscorpions: (**a**) *Chthonius delmastroi* was described the first time in 2009 in Italy; (**b**) *Rhacochelifer maculatus* was discovered by the famous entomologist and arachnologist Ludwig Carl Christian Koch in 1873; (**c**) *Roncus sardous* owes its name to the Italian island Sardinia where it was first discovered; (**d**) *Neobisium* (*Ommatoblothrus*) *zoiai* belongs to a genus of pseudoscorpions which includes over 230 different species. (SZO)

Macrofauna – Formicidae

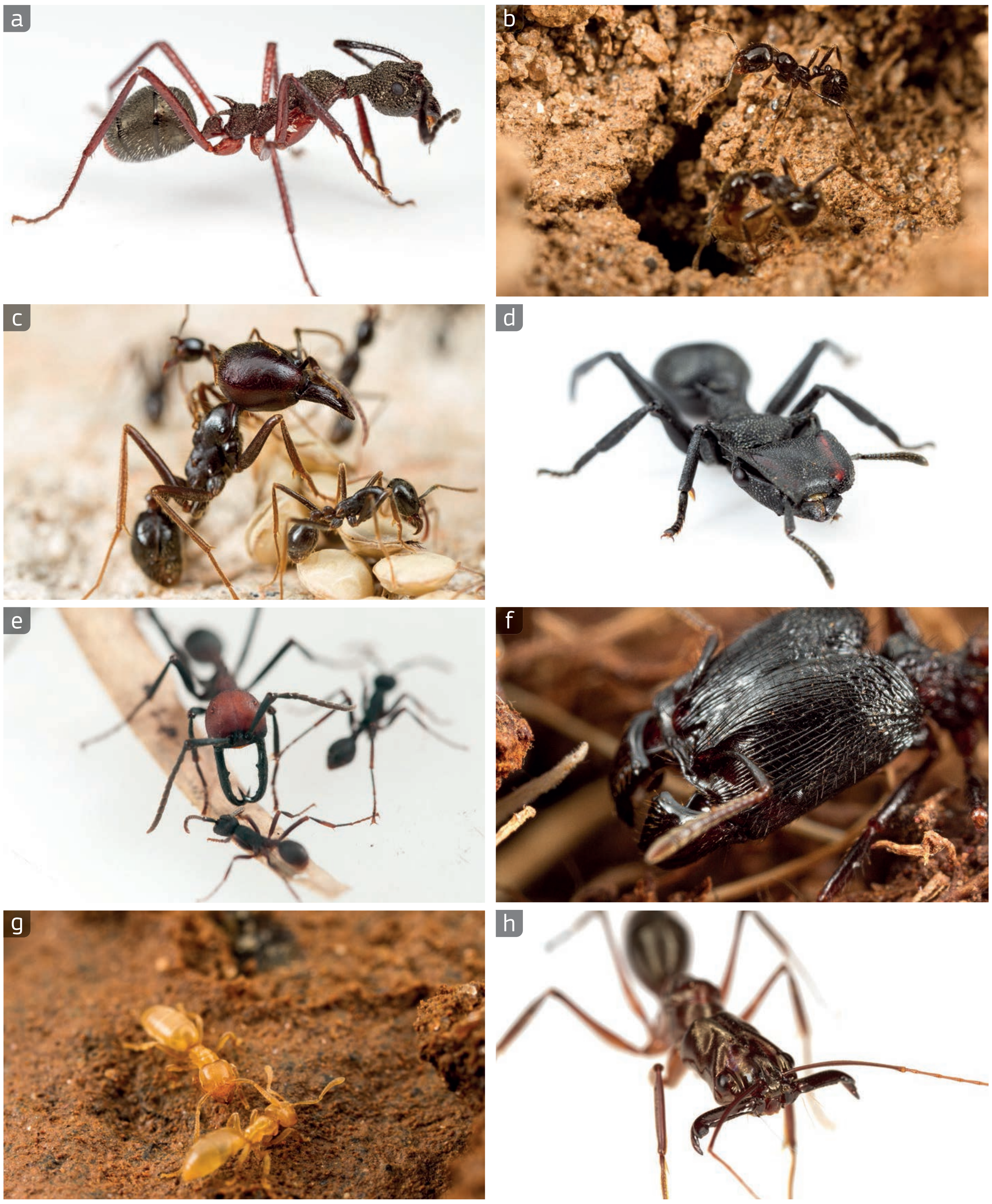
Morphology

Ants are social insects, among the most abundant in the world. Many ants have a sting but some groups have lost theirs and instead spray formic acid. They are distinguished from other closely related groups by the petiole (a constriction between the abdomen and thorax with either one- or two-nodes or scales) and their elbowed antennae. Ants live in large complex colonies with a division of labour, involving reproductive and non-reproductive individuals, cooperative care of the young and overlapping generations. This defines them as eusocial insects. This division of labour leads to different castes (groups of individuals with the same function). The reproductive caste is the queen, while the sterile caste are workers (and in a few species also soldiers). Reproductively active males are produced only during the breeding season and die soon after mating. The workers perform all the other functions of the colony, including protection, foraging, cleaning, building nests and care of the larvae. [60, 61]

Taxonomy

Ants have been around for over 120 million years. They belong to the family Formicidae of the order Hymenoptera (the group containing also bees and wasps).

Importance of ants in the ecosystem: (**a**) *Pseudomyrmex concolour* is just one of a plethora of ant species that establish very close relationships with trees. This tree is *Tachigali myrmecophila*; (**b**) *Odontomachus* sp. preying on another arthropod; (**c**) *Lasius niger* ant tending aphids. (RRCS, PB, KS)



Diversity of ants, the most species-rich and ecologically diverse group of social insects on the planet: (**a**) *Dolichoderus atellaboides*; (**b**) *Solenopsis* sp.; (**c**) *Labidus praedator*; (**d**) *Cephalotes atratus*; (**e**) *Eciton* sp.; (**f**) *Pheidole fimbriata*; (**g**) *Acropyga goeldii*; (**h**) *Odontomachus* cf. *chelifer*. (RRCS)

Microhabitat

Ant colonies form nests in which the colony lives. In most cases the colony centre is fixed, but some army ants have no fixed colony centre. Ants can have nests that are arboreal (in tree canopies), epigeic (on the soil surface) or hypogeic (underground). Ants that nest underground dig tunnels that are interconnected by larger chambers, some of which give access to the outside world. The chambers can have specific functions, such as nurseries, larders and rubbish dumps. Among the ants that nest in the ground some of the most impressive are the leaf-cutter ants, especially in the genus *Atta*, that build very large nests up to 300 m^2 in surface area, and excavate a great deal of soil. *Atta laevigata* nests may be up to 7 m deep and contain over 7 800 chambers.

'Ant cow' aphids

- Certain aphid (small sap-sucking insects) species have a symbiotic relationship (see box on page 33) with various species of ants, which resembles that of domestic cattle to humans; hence the name 'ant cow'.
- The ants tend to the aphids, transporting them to their food plants at the appropriate stages of the aphids' life cycle and sheltering their eggs in their nests during the winter.
- The aphids, in turn, provide sugary secretions (honeydew) for the ants to feed on.

Many ants are predators or herbivores, but others are omnivorous (with a diet consisting of a variety of food sources) or specialist predators (e.g. on termites). Leaf-cutting ants use leaves as a substrate for their symbiotic fungus (fungus-growers), which they use as food source. Ants interact closely with many other organisms and are fundamental for some functions of ecosystems; for example, protection of certain plant species ('ant plants') from herbivory and facilitation of seed germination in appropriate locations by carrying them to their nests. Ants also play an important role in the maintenance and functioning of soils, as they dig tunnels and chambers, thus promoting nutrient cycling through soil bioturbation (the reworking of soil) and water infiltration. They produce soil organic debris, thus enabling the processes of decomposition performed by fungi (see pages 38-41) and bacteria (see pages 33-35) and increasing the heterogeneity of the soil resource.

Diversity, abundance and biomass

The family Formicidae is subdivided into 22 extant subfamilies, 300 genera and 14 000 described species. The diversity of species varies among world regions, with peaks in South America, Central and South Africa and Australia. They are dominant invertebrates in many ecosystems, particularly tropical ones, and occur on all continents except Antarctica. The biomass of ants in tropical rainforests is often thought to be greater than that of all vertebrates in the rainforest combined.

Macrofauna – Termites

Morphology

Termites are medium to small sized fully social insects (2 mm to 20 mm long). They are soft bodied and of colours ranging from very pale white to deep brown or black. They live inside colonies with two reproductive individuals (i.e. the king and the queen) and a very large number of sterile castes (i.e. workers and soldiers). The soldiers and workers look very different from the reproductive castes. The workers do most of the various tasks required by the colony (e.g. rearing young, foraging for food, nest building), while the soldiers defend the colony and have no other roles. [62]

Taxonomy

Termites are hexapods (see page 31) that form the order Isoptera, including 12 families. Termites are a special kind of social cockroach and, despite some similarities in shape and size, they are not closely related to ants. However, similar to ants, they are fully eusocial insects.

Microhabitat

They feed on dead plant material at different stages of decay; for example, dead wood, dry grass, leaf litter and soil. Some form a mutualistic relationship with a fungus called *Termitomyces* that breaks down dead plant material for the termites, who then eat parts of the fungus. Because of these food preferences, a few are serious timber and crop pests. However, most termites have a generally positive effect on ecosystems, living and feeding in the soil where they transform its structure, decompose plant residues, and help stabilise soils. They perform many of the same functions as earthworms, but the two groups are generally not found in large numbers together. They are often known as ecosystem engineers (see box on page 95) as they profoundly affect the structure of habitats for other organisms, both inside and outside their nests.

Diversity, abundance and biomass

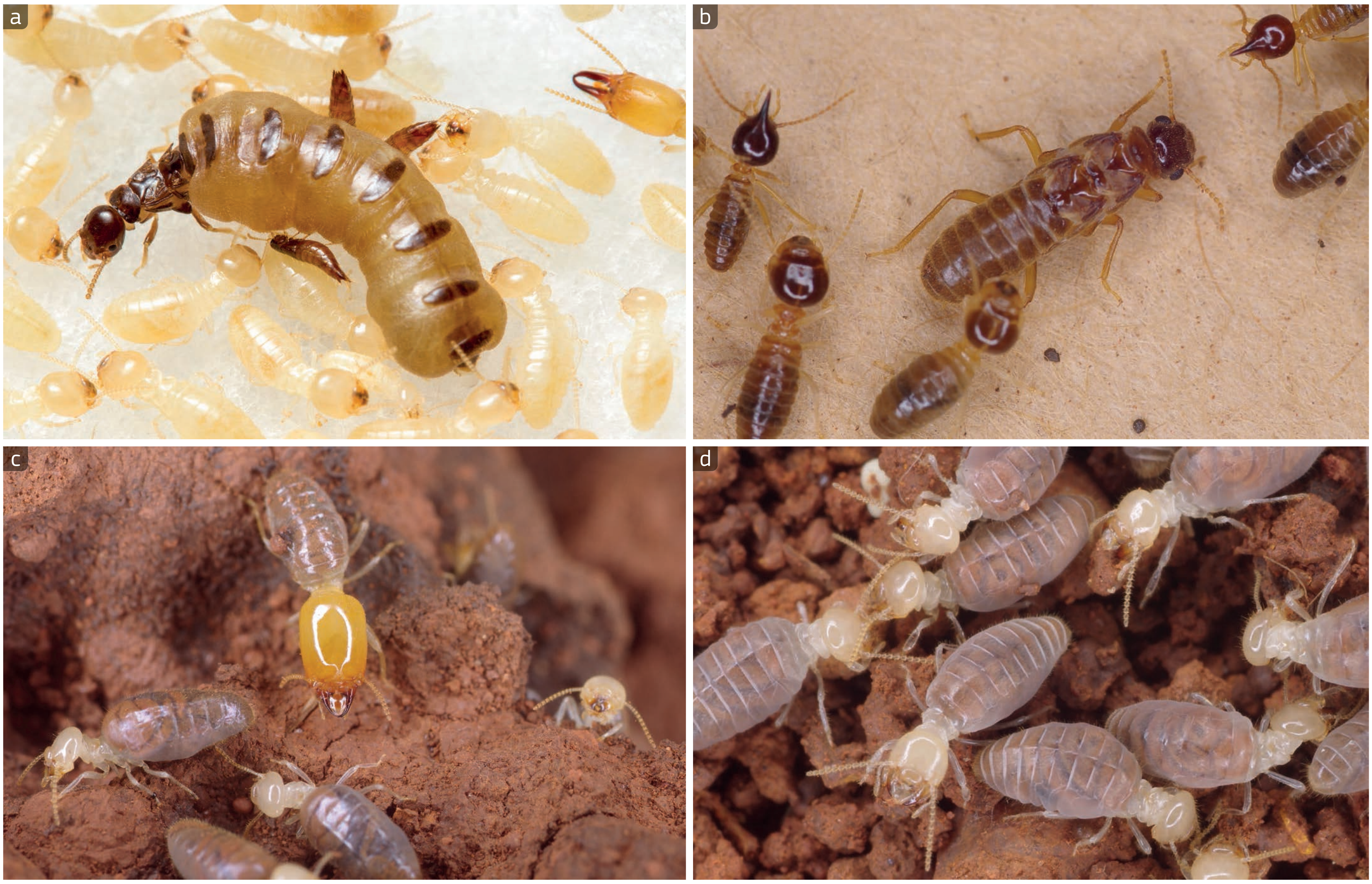
There are about 2700 described species. They are found in very large numbers throughout the warmer parts of the world, particularly in tropical rain forests, tropical savannahs and hot arid areas; they are not found, however, in many temperate regions and never in polar ones. They have their highest densities and diversities in tropical rain forests in Africa where they can reach up to 10000 individuals per square metre (m^2) and biomasses of up to 100 grammes per m^2.

Extraordinary architects

- Termites move around in tunnels in the soil or live entirely in tunnels in dead wood.
- They are nature's most accomplished non-human architects and build nests and mounds of extraordinary complexity, such as those in savannahs in Africa, South America and Australia.
- Some termite mounds may have been continuously occupied for 50000 years.

A termite mound in Australia. Mounds can be very large, up to 9 metres high. These nests are also known as termitaria. The structure of these mounds can be quite complex, including several chambers. (BJ)

Termite-feeding effects. (**a–b**) Termites' diet is mainly based on cellulose, i.e. wood. (**c**) Some termite species can damage unprotected buildings and other wooden structures. (MTB, SG, ST)



Termites live in colonies that are organised in castes. (**a**) A queen of the species *Reticulitermes flavipes* and (**b**) a king of *Nasutitermes coxipoensis*. They represent the reproductive caste. In some species, the mature queen has a greatly distended abdomen and may produce 20000 to 30000 eggs per day. A termite queen can live up to 45 years. The king grows only slightly larger after mating and continues to mate with the queen for life. (**c**) Soldiers defend the colony against enemies (such as ants) using their enlarged jaws and defensive chemicals secreted by specialised glands (in this image, one soldier and several workers of *Labiotermes brevilabius*). (**d**) Workers are numerically dominant in the colony and are responsible for foraging, food storage, brood care and nest maintenance (in this image, workers of *Anoplotermes* sp., a soldierless termite). (MBE, RC)

Macrofauna – Isopoda

Morphology

Most species of isopods belong to the soil macrofauna, and adult sizes range from 5 to 15 mm, with some species reaching only 1 to 2 mm. Terrestrial isopods, commonly known as woodlice or pill bugs, have bodies divided into a cephalon (head), pereion (thorax) and pleon (abdomen). The cephalon bears the compound eyes, two pairs of antennae (one pair is vestigial, meaning functionless) and four pairs of mouthparts for food processing. The pereion has seven pairs of walking legs (pereiopods). The abdomen comprises five pairs of modified appendages (pleopods). The pleopods have become modified and adapted for respiration through the course of isopod evolution. In males, the first two pleopods are modified to participate in sperm transfer. The sperm is transferred to the female through the modified second pleopod which, after receiving the sperm from the penis, is then inserted into a female gonopore (genital pore). After successful copulation, the female moults and produces a structure on the ventral side of her thorax that resembles a pouch and is called marsupium. Inside the marsupium the eggs stay protected while they develop into young independent isopods. [63]

Taxonomy

Isopoda is an order of crustaceans (see page 31). The semi-terrestrial and 'truly' terrestrial isopods form a monophyletic (developed from a single common ancestral form) group (the suborder Oniscidea), with 3 637 described species.

Microhabitat

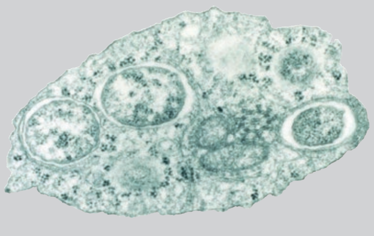
Numerous morphological, anatomical and physiological adaptations to the soil environment make isopods the most successful land inhabitants. Terrestrial isopods occupy essentially all terrestrial habitats, ranging from the supralittoral (shore of a lake, sea, or ocean) to the high alpine regions, from the tropics to the cold-temperate zones, from wetlands to deserts. They are crepuscular or nocturnal animals and spend the day mostly hidden underneath stones, coarse woody or loose bark, or in crevices, where they can easily be captured. In deserts, species of the genus *Hemilepistus* form monogamous (having a single partner during their lives) relationships and live inside self-dug burrows essential for their survival. As macro-detritivores, terrestrial isopods significantly contribute to decomposition processes through feeding on and digesting leaf litter, dispersing microbial spores and mediating microbial activity and nutrient cycles (see pages 102-106). Digestion is supported by microbes that are ingested together with food. In their gut, isopods can also develop symbiotic relationships with bacteria, but at least some part of the cellulose digestion seems to be facilitated by endogenous enzymes (cellulases). Gut bacterial symbionts live protected inside the digestive glands, which enables them to survive on nutrient-poor diets that are difficult to digest.

Diversity, abundance and biomass

The Mediterranean region is a hotspot of isopod diversity, and Europe is the most studied region. Relatively little is known about terrestrial isopods in many tropical countries. Regional species richness increases from the cold-temperate to the warm-temperate and the tropical zones. Local abundances are quite variable and are particularly high in temperate forests and grasslands, reaching about 100 to 600 individuals per square metre.

Isopod manipulators

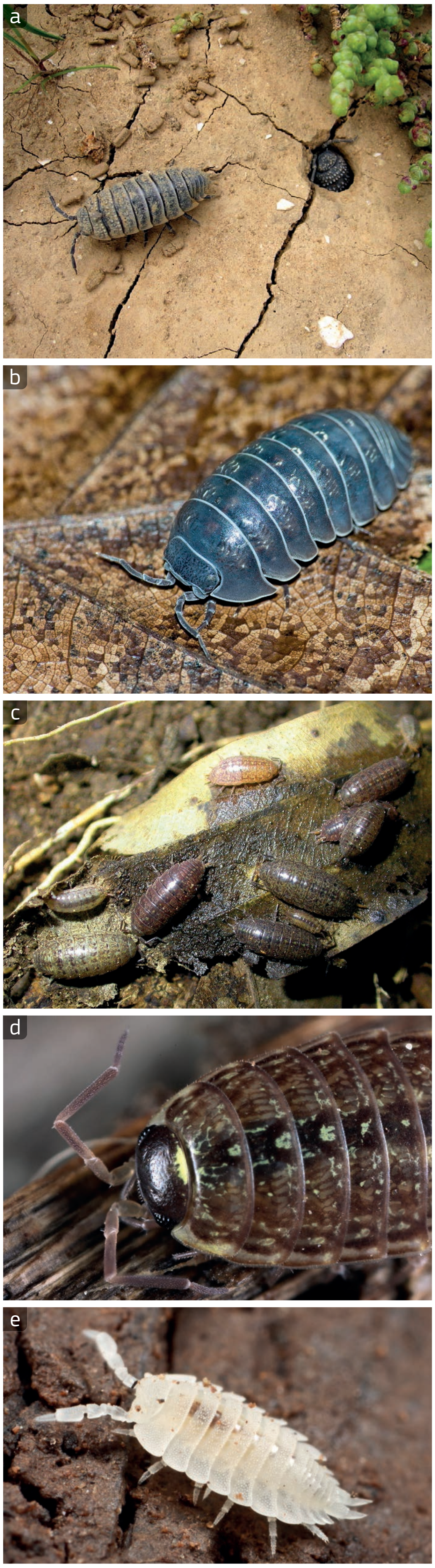
- Bacterial symbionts, such as *Wolbachia*, can induce sex changes and force males to develop into functional females.
- Parasitic acanthocephalan worms can manipulate the pigmentation and behaviour of the infected individuals.



A bacterium of the genus *Wolbachia*. These bacteria are sex manipulators not only in isopods but also in insects and nematodes. The mechanisms responsible for the manipulation are still under investigation. (SO)

The typical segmented body gives some species of terrestrial isopods the flexibility to be able to curl into a ball to protect themselves from danger. Despite this, the woodlice are preyed upon by a number of animals. Toads, spiders, millipedes and the occasional wasp are the main predators of the woodlouse. (DT)

A live specimen of the isopod *Porcellio scaber*, a species commonly found in European forests, gardens and composts. It has also colonised North America, South Africa and other areas, largely through human activity. It is also the most common species of isopod found in Australian gardens. (SF)



Diversity of terrestrial isopods. (**a**) The desert isopod *Hemilepistus reaumurii*, in Tunisia. One individual guards the entrance of its burrow against intruders. (**b**) *Armadillidium vulgare*, a species distributed worldwide. (**c**) Neotropical terrestrial isopods *Balloniscus glaber* and *Atlantoscia floridana* (the smallest individual on the picture). *Balloniscus glaber*, similar to many other terrestrial isopods, show diverse forms of body pigmentation and colour polymorphy. (**d**) *Philoscia muscorum* is a common European woodlouse. (**e**) *Platyarthrus hoffmannseggi* usually lives inside ant nests. (AQ, GM, DT, AM)

Macrofauna – Myriapoda

Morphology

Myriapods (centipedes, millipedes, pauropods and symphylans) are small- to large-sized arthropods (0.5 - 385 mm) with elongated segmented bodies and many legs (from eight pairs up to 750 pairs). Myriapods' bodies have a head and a more or less uniformly segmented trunk. Millipedes have fused pairs of segments (diplosegments) and, consequently, they have two pairs of legs per segment. Centipedes have forcipules, the first pair of modified walking legs on their trunk segment that contain venom glands to catch and immobilise prey. Pauropoda are very small and have branched antennae with segmented stalks. By contrast, Symphyla have a pair of conical cerci with spinning glands on the posterior part of their body. [64, 65]

Taxonomy

Myriapods (phylum Arthropoda, subphylum Myriapoda) are categorised into four classes: Diplopoda (millipedes, 16 orders, approximately 12 000 species), Chilopoda (centipedes, five orders, approximately 3 000 species), Pauropoda (two orders, approximately 800 species) and Symphyla (one order, approximately 200 species). The most diverse orders are: Polydesmida (flat-backed millipedes, 3 500 species) and Geophilomorpha (soil centipedes, 1 300 species).

Microhabitat

Generally, myriapods are soil dwellers. Larger species burrow, while smaller and thinner species use crevices and spaces in the soil. They can be found in both deep and shallow soil layers. They all thrive at high humidity, stable temperatures and low ultraviolet radiation levels; therefore, they are typically found under stones, logs and barks, and in litter, in tree hollows, stumps and caves. Some species of millipedes and centipedes can climb trees.

Diversity, abundance and biomass

Myriapods are found in almost all terrestrial habitats from deep soil layers and caves to above the timberline in mountains. Antarctica is the only continent with no myriapods. Myriapods are not exceptionally abundant in any habitats, with the exception of some millipede species. In temperate regions, the abundance of millipedes can reach up to tens to several hundred individuals per square metre (m^2). In some temperate forest soils, millipedes can reach densities of over 1 000 m^2. Symphylans and pauropods are distributed more unevenly, and in lower abundance since they are very responsive to changes in soil properties (chemical as well as physical) and food availability. Different myriapod groups have different feeding preferences. Centipedes are generally predators and often regulate populations of smaller animals, although some feed on decaying plant matter. Symphylans are root-feeders, or saprophagous. Pauropods are fungal-feeders, although some species prey on small animals or suck liquids from rotting plant material. Millipedes are important decomposers of leaf litter. They are estimated to break down 10 - 15 % of the annual leaf fall, and their significance for litter processing is higher than that of earthworms in boreal forests.

Poisonous, luminous and singers

- Although centipedes are venomous and sting frequently, the United States National Center for Health Statistics reports only five 'possible' deaths attributable centipede stings in the US between 1991 and 2001.
- Almost all millipedes have defensive poisonous liquid secretion or produce prussic acid (hydrogen cyanide) gas.
- Some species of millipedes are bioluminescent, allowing them to be avoided by nocturnal predators. This luminescence may be the equivalent of colours used in other animal species to warn off potential predators (aposematic colours).
- A defense mechanism of some millipedes is to roll into a ball. Consequently, a male may find it hard to persuade a female to copulate.
- Although millipedes are deaf, males of the order Sphaerotheriida 'sing' to potential mates using vibrations in order to uncoil them.
- Some centipedes inhabit tidal zones, probably in search of food. In Brazil, there is a documented record of a sea anemone species feeding on a centipede belonging to the family Scolopendridae.
- The largest millipedes in the world are the African giant black millipedes (*Archispirostreptus gigas*) which may reach 30 cm. They have approximately 256 legs and a life expectancy of five to seven years.

Diversity of Diplopoda and Chilopoda. (**a**) Some millipedes, like this *Castanotherium* sp. from Bornean rainforests, can coil into a tight ball in response to intruders. (**b**) *Gigantomorpha immanis* from Brunei. Flat-backed millipedes produce acid as a defence against predators. They also warn predators using intense colouration. (**c**) *Scolopendra cingulata* is a soil centipede that frequently stings humans in southern Europe. Sharp claws inject venom into prey. The venom of some species is ranked among the most painful toxins on Earth. (**d**) Stone centipedes inhabit stony debris, litter layers and caves, but some species, like this European *Lithobius melanops*, frequently enter into buildings. (IHT, FT)

(**a**) Pauropoda and (**b**) Symphyla are the two groups of myriapods with less known species. Pauropoda possess unique forked antennae, whereas Symphila have characteristic long and moniliform (i.e. resembling a string of beads) antennae. (AM)

Macrofauna – Earthworms

Morphology

Earthworms are segmented animals with coelom (coelomates). The body is divided into two parts: an anterior part with segments containing cephalic ganglions, reproductive organs, foregut, calciferous glands and hearts, and a posterior part with a series of similar segments which contains the intestine. Earthworms range from a few cm to 2-3 m long, with most species falling into the range of 5 to 15 cm. Size varies considerably within single species populations, and the largest adults may be more than 100 times those of newly hatched individuals. [66, 67]

Taxonomy

Earthworms belong to the phylum Annelida (class Clitellata, subclass Oligochaeta). The Oligochaeta contain 10 400-11 200 species in approximately 800 genera, and 38 families comprised of approximately 7 000 true earthworms.

Microhabitat

Earthworms have been classified into three main functional groups, each with a preferred habitat:

a. epigeics, which live in the litter layer, a relatively harsh and exposed environment. They are small and uniformly coloured worms, pigmented green, blue or reddish depending on whether they inhabit grassland or forest. They counterbalance a high mortality rate with high quality food (leaf litter), which allows them to grow and reproduce rapidly
b. anecics feed on surface litter that they mix with soil. They live in vertical subterranean tunnels created within the soil. They are large worms with a dark pigmentation and strong anterior digging muscles. They are long lived, with low growth and mortality rates
c. endogeics are unpigmented soil-feeding worms that live entirely within the soil, which is a more buffered and predictable environment than the leaf litter, but where the quality of the food is much lower. They have also developed different ways of exploiting it. They include small filiform earthworms that selectively ingest fine organic rich soil (polyhumics), medium-sized ones that ingest soil with no selection (mesohumics) and the very large ones that live down to a 30-60 cm depth where the extremely low quality of their food is compensated for by steady environmental conditions (oligohumics)

Diversity, abundance and biomass

Although 7 000 'true' earthworms (in 20 families) have been described to date, the total is probably around 30 000 species globally. They live everywhere except in dry and cold deserts. They are, however, mostly found in soil and leaf litter, although they occasionally climb trees and can live in suspended soils of epiphytic plants (that grow on other plants). Local species richness is often as low as 10 or fewer, although it may reach 15 species in well conserved soils of temperate regions and a maximum of 40-50 in some tropical regions. Density is often in the range of 100 to 500 individuals per square metre and may reach 2 000 in temperate pastures of New Zealand or irrigated orchards in Australia. Live biomass commonly ranges between 30 and 100 grammes (g) per square metre, with maximum values of 200 g to 400 g.

Rescuers, hermaphrodites and carnivores

- Earthworms are able to produce plant growth hormones and to modify the expression of plant genes. They may, for example, render a plant tolerant to plant parasitic nematodes (see pages 45-46) by inhibiting the gene responsible for the repair of damaged roots, preventing plant death after all leaves have wilted.
- While several cosmopolitan species are parthenogenetic (virgin births), the majority are hermaphrodites as they can produce progeny after the mating of two sexually mature specimens. Sperm stored in specific structures (spermathecae) fertilise eggs produced by the same individual when the female reproductive system matures.
- Earthworms may ingest up to 20-30 times their own weight of soil every day, and more than 1 000 tonnes of dry soil a year.
- In West Africa, the genus *Agastrodrilus* has been shown to be carnivorous, feeding on smaller worms.
- The title for the largest earthworm in the world, with a length of 2.9 m, is claimed by *Amynthas mekongianus*, about the same as large *Megascolides australis*, the 'Giant Gippsland Earthworm'.

Diversity of earthworms: (**a**) *Pontoscolex corethrurus*, the most widespread earthworm in disturbed soils of tropical areas; (**b**) *Pheretima philippina* from the Philippines; (**c**) a luminescent *Amynthas* sp. from Japan; (**d**) *Glossoscolex* sp. from Brazil; (**e**) a specimen belonging to the family Microchaetidae; (**f**) a specimen belonging to the family Acanthodrilidae from South Africa; (**g**) Giant *Buettneriodrilus* sp. from Gabon; (**h**) *Martiodrilus tenkatei* from French Guiana; (**i**) *Martiodrilus* sp. from French Guiana; (**j**) *Nouraguesia* sp. from French Guiana. (PL, SJ, SMI, TD)

Macrofauna – Coleoptera

Morphology

The defining feature of beetles (Coleoptera) is the hardened forewings (elytra) that cover their body. The largest known beetles are more than 160 mm long (e.g. *Dynastes hercules*), but most beetles are less than 5 mm long. Their colours are variable, although most soil-dwelling beetle species are brown or black. Their body shape is also variable: some have long horns or sharp tusks, some can curl up like myriapods (see page 57), some are flat and some are slim. A number of soil beetles, such as the genus *Carabus*, are wingless. [68, 69]

Taxonomy

Beetles are hexapods belonging to the order Coleoptera. This includes four suborders: Archostemata, Adephaga, Myxophaga and Polyphaga. Of these, Adephaga and Polyphaga have more species than other suborders, including most soil species.

Microhabitat

In terrestrial environments, many beetles can be found in soil, humus and leaf litter, under logs or in decomposing wood, under stones, in dung, carrion and in the fruiting bodies of many types of fungi (see pages 38-41). Numerous beetles (families Carabidae, Leiodidae, Staphylinidae and Scarabaeidae) are well adapted to the soil environment. Some carrion beetles (family Silphidae) and some dung beetles (family Scarabaeidae) build nests in the soil, in which they take care of their brood. Some species, such as some members of the family Staphylinidae, live solely in caves while others are myrmecophiles (ant lovers) or termitophiles (termite lovers) as they strikingly resemble ants or termites (see pages 54-55) and live in their hives.

Diversity, abundance and biomass

There are more than 370 000 described species of Coleoptera – it is the largest and most diverse order of organisms on the planet, making up about 40 % of all described insect species, and about 30 % of all described animal species. The abundance and biomass of beetles on ephemeral and nutrient-rich resources, such as carrion and dung, are very high. Beetles significantly contribute to decomposition processes. Besides being abundant and varied, soil beetles are able to exploit the wide diversity of food sources that are available in their habitat. Many species are predators of small soil animals such as earthworms, collembolans and nematodes (see pages 46-47, 50, 58). Others feed on fungi or dead wood.

A recent study has shown that the dung beetle *Scarabaeus satyrus* uses the Milky Way to navigate during night time. This is the first known species to do so in the animal kingdom. (KKE)

The caring gravediggers

- Burying beetles bury carcasses of small vertebrates, such as birds and rodents, as a food source for their larvae.
- They are unusual among insects in that both the male and female parents take care of the brood.
- Although parental responsibilities are usually carried out by a couple of beetles, a male or a female may also care for the brood alone, when the other partner is lost or the carcass is small.
- Sometimes more than two unrelated individuals can raise a brood together, when the carcass is large or many potential competitors are present.

The carcass of a mouse which was rolled into a ball by a burying beetle in Japan. Burying beetles belong to the genus *Nicrophorus* and are the best-known members of the family Silphidae. (MN)

Diversity of Coleoptera: (**a**) a male of the dung beetle *Liatongus minutus* has a long horn used for defense; (**b**) the tiger beetle *Cicindela japonica* with its sharp tusks; (**c**) the rove beetle *Ecitophya* sp. from Peru resembles its ant hosts (neotropical army ants) in overall body shape and colouration; (**d**) the beetle *Madrasostes* sp. from Ecuador can curl up when in danger; (**e**) the ground beetle *Trechiama lavicola* has degenerated eyes and hindwings to adapt to cave and underground life; (**f**) a rove beetle *Aleochariinae* sp. (the upper one) living in a termite (lower one) nest; (**g**) the stag beetle *Aesalus asiaticus* from Japan feeds on decaying wood and fungi; (**h**) the beetle *Aspidiphorus* sp. covered by spores of a slime mould feeding on it; (**i**) the burying beetle *Nicrophorus concolour* feeding their larvae. (YA, TK, MN)

Macrofauna – Soil insect larvae

The vast majority of insects, up to 95 % in fact, are linked to the soil during their life cycle. Some lay eggs in the soil or use it as a substrate for overwintering. Due to very specific features of the soil as a habitat, insect larvae have made numerous adaptations to live in this particular environment. According to their life cycle, insects can be classified as holometabolous, hemimetabolous or ametabolous, depending on whether they undergo complete, incomplete or no metamorphosis, respectively (see box below). Larvae of hemimetabolous insects do not undergo substantial changes in their body form; they are often called nymphs and look very similar to adult insects lacking well developed wings and the ability to reproduce. The holometabolous larvae differ greatly from the adult and often occupy different ecological niches. The change to adulthood occurs during pupation. Morphologically, holometabolous insects are very diverse and cover a wide range of trophic levels, from detritivores to herbivores and predators. Among different species, they may vary from less than 1 mm to 12 cm. [70, 71]

Hemiptera larvae

Cicada nymphs (Hemiptera) may be among the most well-known, most likely due to their long life in the soil and huge biomass. They feed by sucking sap from roots and can live in the soil for up to 17 years. Emergence of over 300 nymphs of periodical cicadas per square metre represents the highest recorded biomass (up to 4 000 kilos per hectare) for any terrestrial animal.

A nymph of cicada. Cicadas live underground in this form for most of their lives, at depths ranging from about 30 centimetres down to 2.5 metres. Eventually, they construct an exit tunnel to the surface and emerge. (GW)

Metamorphosis

- The word 'metamorphosis' derives from Greek *meta* (change) and *morphe* (form).
- Metamorphosis refers to a major change in form or structure, usually associated with the development of the wings. One of the most dramatic forms of metamorphosis is the change from the immature insect into the adult form.
- Metamorphosis is sometimes accompanied by a change of habitat or behaviour.
- In insects there are different types of metamorphosis. The principle is that metamorphosis is closely linked to wing development; therefore:
  - ametabolous are wingless insects (apterygota), so they do not develop wings (no metamorphosis);
  - hemimetabolous insects have wings that develop gradually (incomplete metamorphosis);
  - holometabolous insects have wings that develop during the pupation period (inactive) where the insect undergoes dramatic physiological and morphological changes to acquire the wings and to feed on different things (complete metamorphosis).
- In hemimetabolous insects, immature stages are called nymphs. Development proceeds in repeated stages of growth and moult (ecdysis); these stages are called instars. The juvenile forms closely resemble adults but are smaller and lack adult features, such as well developed wings and genitals. The differences between nymphs in different instars are small, often just differences in body proportions. Examples of the hemimetabolous insects are: aphids, cicadas and leafhoppers.
- In holometabolous insects, immature stages are called larvae, and differ markedly from adults. Insects that undergo holometabolism pass through a larval stage, then enter an inactive state called pupa, or chrysalis, and finally emerge as adults. Examples of the holometabolous insects are: beetles, flies, ants and bees.

Diptera larvae

Diptera larvae in general look like small worms as they are all legless. However, their ecological functions are very diverse. Some of them mine taproots (see page 43) and feed on the internal cortex. Others live in litter or dung, which they decompose.

Dipteral larvae show diverse feeding habits. (**a**) Larvae of *Delia radicum* (the cabbage fly) feed on the cabbage plant taproot. (**b**) Dipteral larvae (family Bibionidae) living in litter. (TT)

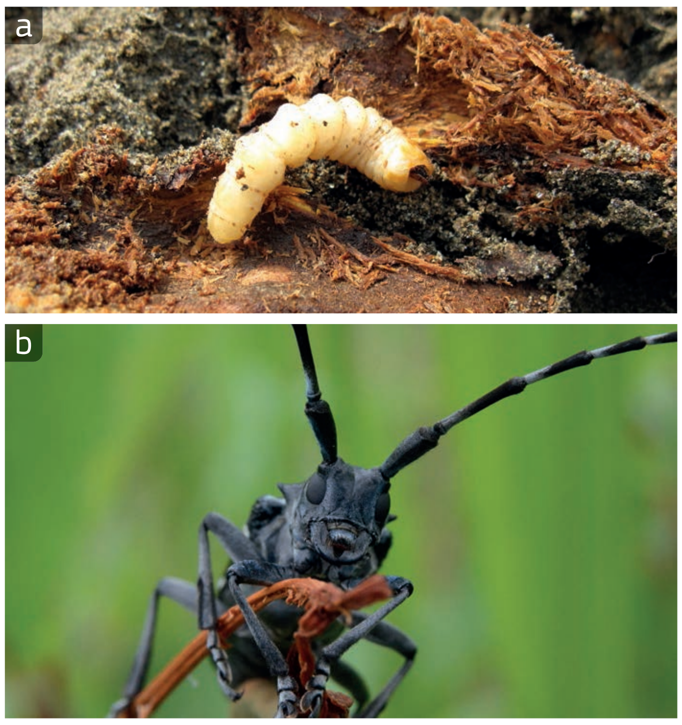
Lepidoptera larvae

Lepidoptera larvae show diverse feeding strategies. The majority feed on green plants. Ghost-moth larvae in Tibet dig soil and feed on live roots. They are often infected by a caterpillar fungus (*Ophiocordyceps sinensis*, Ascomycota) valued in herbal medicine. Some others live in ant colonies, and are fed mouth-to-mouth by ants, or feed on residuals of ant food.

Some Lepidoptera larvae in the soil have interesting relationships with other organisms. (**a**) *Ippa conspersa* larvae in their figure-eight-shaped shell. They are scavenging around an ant nest. (**b**) A mushroom-like structure with a bright orange head of the parasitic fungus *Cordyceps militaris* growing from a Lepidoptera pupa. (TT)

Coleoptera larvae

Coleoptera larvae are represented by hundreds of families with different feeding habits. Some longhorn beetle larvae (Cerambycidae) bore into roots or rhizomes. Click beetles and scarabaeid larvae chew fine roots or decaying plants. Some scarabaeid larvae are parasitised by Hymenoptera. Tiger beetle larvae (Cicindelidae) live in cylindrical burrows, and wait for their prey to pass by on the soil surface.



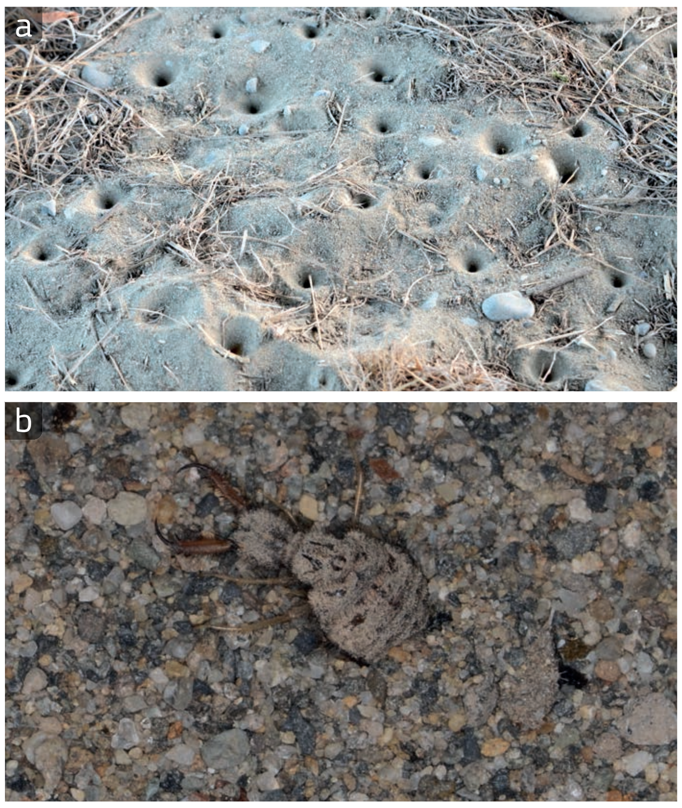
The Coleoptera species *Anoplophora malasiaca*. (**a**) Larva, which undergoes complete metamorphosis, and lives in plant roots, is very different from (**b**) the adult. (TT)

One works, the others feast

- Some parasitic species undergo hypermetamorphosis, which refers to a class of variants of holometabolism. In hypermetamorphosis some larval instars (usually the first one) are functionally and morphologically distinct from each other.
- In the beetle family Meloidae, the first instar is called triungulin (as it has three claws on each foot) and actively seeks out prey on which subsequent instars feed.
- Triungulin is elongated and flattened and in this form it does not feed. When it finds its prey it moults, transforming into a scarabaeiform or vermiform larva that does not hunt, but feeds.

Neuroptera larvae

Most Neuroptera larvae are predators, with elongated mandibles. By using the mandibles, they catch and pierce prey, and inject digestive juices. Ant lions (family Myrmeleontidae) create pitfall traps, and eat small arthropods that fall in.



Ant lions (Neuroptera) build their (**a**) traps in sand, and (**b**) wait for prey to pass. Ant lion is a name applied to a group of about 2 000 species of the family Myrmeleontidae. (TT)

Macrofauna – Ground- and litter-dwelling macrofauna

Introduction

The soil surface and leaf litter are important components of soil and may represent a perfect habitat. In particular, leaf litter, made up of dead plant material, such as leaves, bark, needles and twigs, that has fallen to the ground, is very rich in nutrients and keeps the soil moist. It also offers the perfect conditions in which to build nests: hiding places and protected spots. Many of the organisms inhabiting the ground and the litter fall within the group of soil macrofauna (animals that are at least one centimetre long). Macrofauna include myriapods, beetles, insect larvae, slugs, snails, spiders and scorpions (see pages 57, 59-60). Some of these organisms spend their entire lives on the soil surface and in leaf litter, while others are found only there at certain points in their lives. These organisms may have a high ecological importance (e.g. as decomposers of litter). In these pages, we focus on the Arachnida (e.g. spiders and scorpions), Gastropoda (e.g. snails and slugs) and some Hymenoptera (e.g. mining bees). [72, 73]

(**a**) The Goliath birdeater, *Theraphosa blondi*, the world's largest spider. (**b**) A specimen of *Habronattus amicus* feeding on a bristletail. (**c**) A trapdoor spider, *Bothriocyrtum californicum*. (**d**) *Homalonychus theologus* has bristles that serve to gather sand/soil particles, thus providing a natural camouflage. (SM, MH)

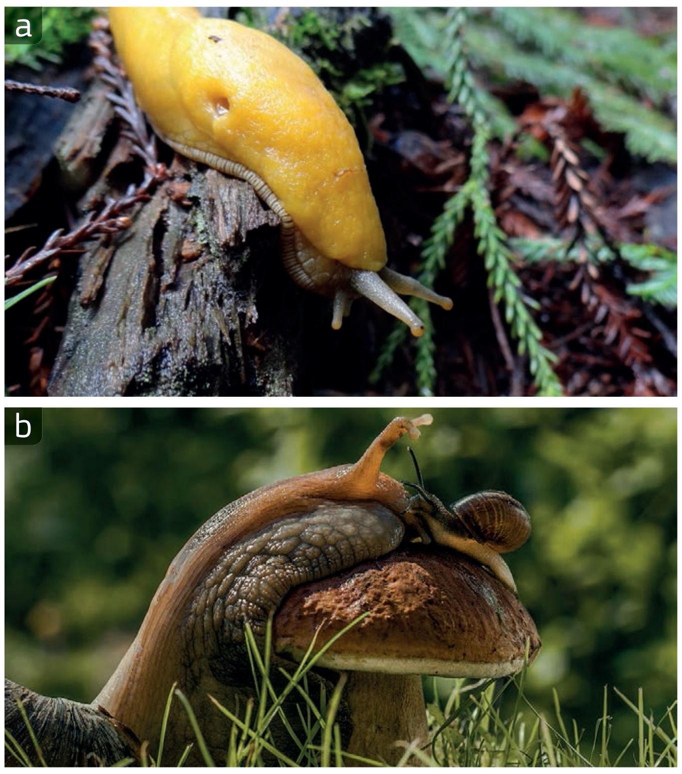
Arachnida

The class Arachnida are arthropods. Their eight legs that distinguish them from insects, which have six legs. The most well-known groups of arachnids are spiders (order Araneae) and scorpions (order Scorpiones). Spiders come in a large range of sizes, from less than 1 mm up to 30 cm, such as the Goliath birdeater (*Theraphosa blondi*), a spider belonging to the tarantula family. Scorpions range in size from 9 mm up to specimens such as the Mexican cave-dwelling *Typhlochactas mitchelli* that can reach up to 20 cm. Spiders' bodies consist of two sections (tagmata): the cephalothorax or prosoma at the front, and the abdomen or opisthosoma at the back. Spiders have a pair of cephalic appendages in front of the mouth (chelicerae), which they use to inject venom into prey from venom glands. Scorpions' bodies are also divided into two regions: the head (cephalothorax), the abdomen (opisthosoma), which is subdivided into mesosoma (seven segments) and the metasoma or tail (five segments plus a sixth, the telson, bearing the sting). The sting consists of the vesicle, which holds a pair of venom glands, and the aculeus, the venom-injecting barb. Spiders make up a very large group of organisms comprising more than 40 000 species. About 1 700 species of scorpion have been recordered to date. Spiders and scorpions are found on all major land masses, except Antarctica. Both groups are predators. They mostly prey on insects, although a few large species can also take lizards, birds and small mammals. An exception is represented by the herbivorous spider species *Bagheera kiplingi*. Soil is often used as their hunting ground, in which they use different methods of capturing prey. One of the most clever strategies is adopted by the ambush 'trapdoor spiders' (family Ctenizidae); they burrow holes into the soil, often closed by trapdoors and surrounded by networks of silk threads that alert these spiders to the presence of prey. Scorpions are nocturnal hunters, remaining in underground holes or under rocks during the day. Scorpions can survive long periods of food deprivation thanks to a specific food-storage organ and slow digestion process; some are able to survive 6-12 months of starvation.

(**a**) The scorpion *Vaejovis carolinensis* showing its sting and chelate pedipalps. (**b**) A scorpion feeding on its prey using its chelicerae. (**c**) Before the first moult, a scorpion's brood cannot survive without the mother, since they depend on her for protection and to regulate their moisture levels. (MH, TIW, FK)

Gastropoda

Snails and slugs are the two most relevant groups of gastropods related to soil. Taxonomically, they are both included in the order Pulmonata. The clear difference between them is the presence of a conspicuous shell in snails, which is very reduced, totally absent or internal in slugs. A snail's shell is made of calcium carbonate and has the typical spiral shape. Both snails and slugs range greatly in size; the largest species can reach 30 cm. Around 25 000 snail species are present worldwide, whereas only approximately 5 000 slug species exist. Terrestrial snails are usually herbivorous; however, some species are carnivores. Most slugs feed on a broad spectrum of organic materials, including leaves from living plants, lichens (see page 42), fungi (see pages 38-41) and even carrion. Some slugs are predators and eat other slugs and snails or earthworms (see page 58). Some snail and slug species can cause damage to agricultural crops and garden plants and are, therefore, often considered as pests.



(**a**) A banana (*Ariolimax californicus*) slug. This nickname is due to the colouration. (**c**) Two snails (*Helix* spp.) feeding on a mushroom. The spiral shell is their distinctive feature. (BLO, SJE)

Burrowing or mining bees

- Not all bees (Arthropoda, Ectognatha, Hymenoptera) live in hives like honey bees do and, in fact, five of the seven recognised families of bees are ground-nesting bees (approximately 70 % of the 20 000 known bee species). Their burrows can reach 60 cm in depth and the entrance is often marked by a small mound of excavated soil. Depending on the species, the female fills the brood cells at the end of the branched burrow with pollen, honey or a mixture of nectar and pollen and, once the clump reaches the right size (sometimes after a good number of trips to flowers), she lays an egg on each one. The larva hatches within a few days, grows quickly and pupates within a few weeks. The adults emerge the following spring after hibernation.
- Unlike social bees and wasps, ground-nesting bees do not live in colonies, although some species could nest in large groups ('gregarious nesters') and become so visible, especially in lawns and paths, that gardeners consider them as pests. However, in reasonable numbers they will not harm your garden. They are not aggressive insects even though the females do have stings.
- These solitary bees (specifically *Colletes* and *Andrena*, two common widespread genera) are good pollinators of economically important plants. They are often 'oligolectic', meaning that they collect pollen from only a select few plant species, and if that plant becomes rare or extinct, so does its pollinator.

A bee emerging from its nest in the soil. (JB)

Megafauna – Mammalia, Reptilia and Amphibia

Morphology

Although the soil animals considered as megafauna are not actually large on a human scale, and rarely exceed 1 kg in weight, they are exceptionally 'huge' (usually more than 10 cm long) compared to other soil organisms. These animals often have a morphology adapted to digging and life underground (fossorial life style): e.g. long claws, short tail and/or hair (sometimes hairless) for mammals and a flat, slender, or limbless body to creep in soil/litter for amphibians and reptiles. They sometimes have very tiny eyes or have even lost them altogether. The latter animals develop special organs, such as sensory hair/tentacles, bioelectric receptors, sensitive noses and even echo-location systems like bats, in order to detect their prey in darkness. [74]

Mole claws are apt for digging and, thus, life belowground. (DH)

Taxonomy

Almost all mega soil animals are vertebrates; therefore, 'soil megafauna' is nearly equal to 'soil vertebrate'. Vertebrates are animals that are members of the subphylum Vertebrata, meaning that they have backbones. Small mammals (class Mammalia), such as moles (family Talpidae), shrews (family Soricidae) and some rodents (like the naked mole-rat) are regarded as soil megafauna as are adult salamanders, caecilians (class Amphibia), and blind snakes and limbless lizards (reptiles, class Reptilia) that superficially resemble earthworms or snakes. These vertebrates utilise litter and soil as both habitat and feeding site. Some mammals, such as hares, rabbits, hedgehogs and foxes may build their dens in soil, but are not part of the soil megafauna. Vertebrates that can be included in soil megafauna are only those that use underground space as both habitat and feeding site.

The golden moles

- Golden moles are small burrowing mammals native to sub-Saharan Africa.
- Their fur colour varies from black to pale tawny-yellow, hence their nickname.
- There are 21 different species of golden moles, and more than half of them are threatened with extinction.
- They are taxonomically distinct from true moles and are regarded as rather 'primitive' creatures.

(**a**) Molehills indicate the presence of moles in the soil. Several species of moles (family Talpidae) exist, for example: (**b**) the European mole (*Talpa europea*). Their fur is usually dark grey and their eyes are very small and hidden; (**c**) the Japanese mole (*Mogera imaizumii*) lives exclusively in Japan and was discovered in 1957; (**d**) the American shrew mole (*Neurotrichus gibbsii*) is the smallest North American mole; (**e**) the star-nosed mole (*Condylura cristata*) is another North American species. The specimen shown here is from Canada and uses soil, ponds and streams as feeding grounds. (TR, BK, MAI, SC, CA, KC)

Microhabitat

Moles are known for denning in soil; they continuously build on underground tunnel systems as they burrow in search of food. Moles dig two basic types of tunnel: shallow, surface runways, and deep, more permanent tunnels. In addition, moles construct nest and rest chambers. Surface runways may be used only once; others are used frequently as main travel lanes, called main runways, and may be used for many years. Tunnels occur generally from 15 to 60 centimetres underground – deep enough to be below the winter frost line and to remain cool during summer heat. They are used regularly during the mole's travels between its nest and rest chambers and surface runways. A molehill is built of dirt excavated from these deep tunnels, deposited on the surface in a volcano-shaped mound through a lateral tunnel. Nest and rest chambers are enlargements of a deep tunnel. Nests are made of coarse grass and/or leaves and are often located in protected areas underneath boulders or trees. Soil is also the perfect source of food for megafauna. Both moles and shrews have great appetites for soil invertebrates due to their high metabolic rate. Earthworms, termites, ants, insect larvae, centipedes and isopods (see pages 54-60) are the main prey for soil vertebrates. In addition, they often eat caterpillars and terrestrial snails. An exception is the naked mole-rat that mainly feeds on the tubers of plants [75]. Therefore, predation pressure of moles and shrews on populations of soil invertebrates seems not to be negligible, with an important role in soil food webs (see page 96). Furthermore, the carcasses and feces of soil vertebrates are a high-quality source of nutrients and energy for invertebrates and microorganisms in the soil. Soil megafauna potentially affect the community structure of soil invertebrates not only through their predation, carrion and feces, but also through modification of soil structure by digging activity (typical of moles). In the soil food web, soil vertebrates are tertiary consumers, sometimes also known as apex predators, as they are usually at the top of the food chain. In the aboveground food chain, soil vertebrates are preyed upon by predatory vertebrates, such as carnivorous and omnivorous mammals, raptors, owls and larger reptiles.

Some shrews can be considered as soil-dwellers. For example, the short-tailed shrew (*Blarina brevicauda*) prefers to tunnel belowground, contrary to other shrews. It is also known as one of the few venomous mammals. (SDR)

The pocket gophers

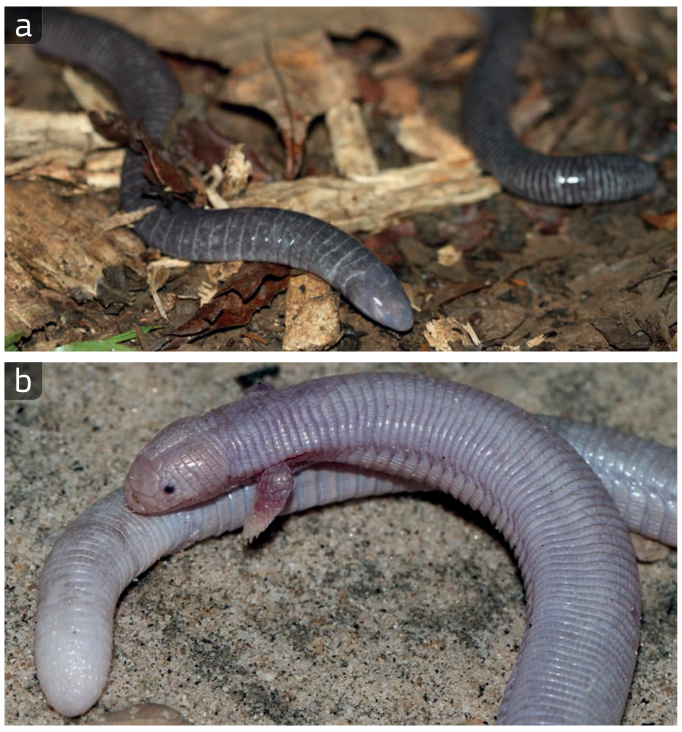
- Pocket gophers are burrowing rodents of the family Geomyidae, including 35 species. They live only in Central and North America.
- They create networks of tunnels that provide protection and a place for food collection.
- They are solitary animals, herbivores (they only eat roots, bulbs and other fleshy portions of plants). Some species are considered agricultural pests.

A Botta's pocket gopher (*Thomomys bottae*). They inhabit a range of habitats, including woodlands, shrublands and agricultural land. (CAB)

The only two mammal species known for their eusocial behaviour are soil-inhabiting rodents. Eusocial means that they live in colonies with a division of labour into reproductive (queen) and non-reproductive (workers) groups. (**a**) The naked mole-rat is extraordinarily long-lived (up to 31 years) for a rodent of its size (8-10 cm). (**b**) The Damaraland mole-rat has a body covered by hairs. (SNZ, FWA)

Diversity, abundance and biomass

The family Talpidae includes 17 genera and 46 species. The 385 shrew species are divided into 26 genera. Each species has its own area of distribution. For example, the nine mole species of the genus *Talpa* live in Europe and western Asia. A particular lifestyle influencing the abundance of a soil-dwelling animal, is that of the naked mole-rat (*Heterocephalus glaber*), the first known eusocial mammal. The only other known eusocial mammal is the Damaraland mole-rat (*Cryptomys damarensis*). Naked mole-rats live in colonies like ants and termites (see pages 54-55), with members responsible for different roles. Only one female (the queen) and one to three males reproduce, while the other members of the colony function as sterile workers. Smaller workers focus on collecting food and maintaining tunnels, while the larger workers are more reactive in case of attacks. Colonies range in size from 20 to 300 individuals, with an average of 75 to 80 individuals. They live together in complex systems of burrows in arid African deserts. The tunnel systems built by naked mole-rats can stretch up to three to five kilometres in length.

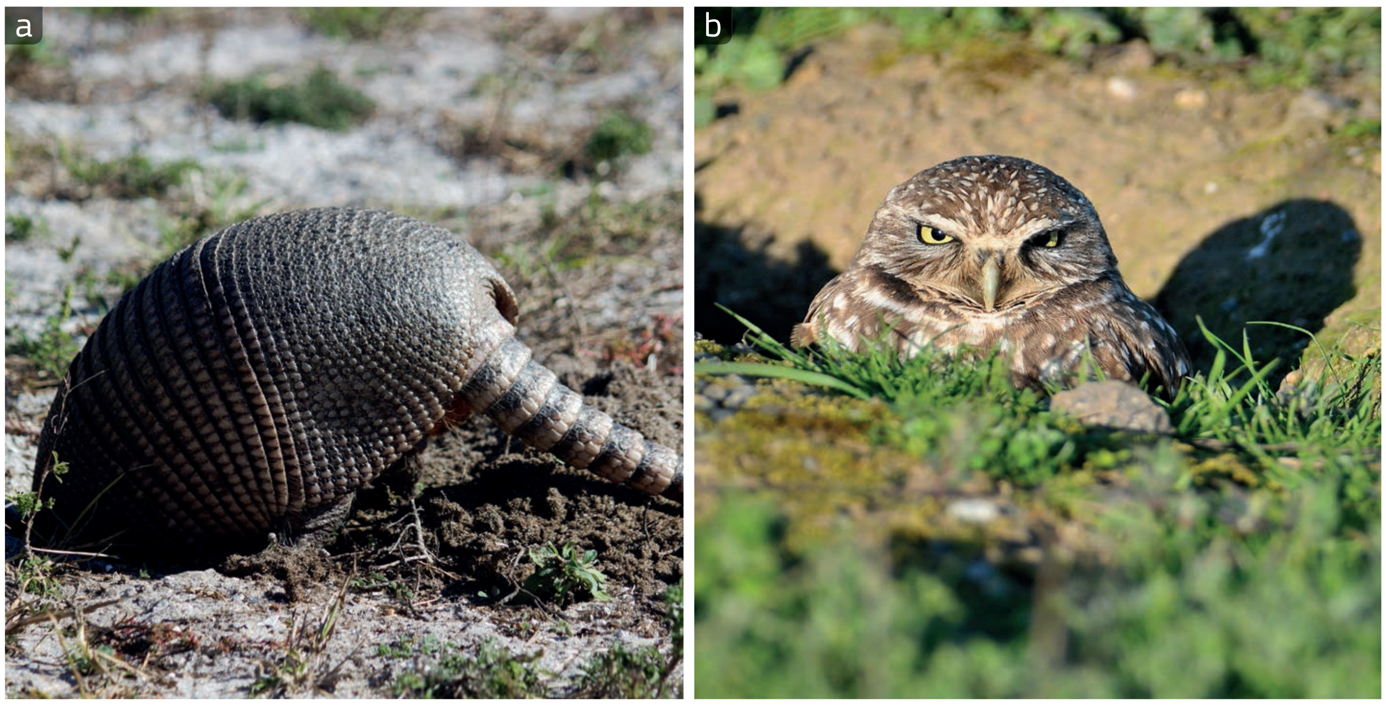


Some amphibians and reptiles can be considered as soil megafauna. (**a**) A caecilian (*Gymnopis multiplicata*) from South America. Caecilians are amphibians that superficially resemble earthworms or snakes. (**b**) The worm lizards are a group of legless lizards (reptiles) that have also adapted to living in the soil. Although the Mexican mole lizard (*Bipes biporus*) has a pair of legs used to burrow, all other genera are limbless. (ACK, DAR)

The star 'nose'

- The star-shaped nose is a unique organ only found on the star-nosed mole (*Condylura cristata*).
- The star-nosed mole's 'nose' is not an olfactory organ (i.e. used for smell), but a skin surface that mediates touch. It is ringed by 22 fleshy appendages, called rays, which are engorged with blood and in a constant flurry of motion when the animal searches for food.
- Innervated by more than 100 000 sensory neurons, the star is probably the most sensitive and highly acute touch organ found on any mammal.
- The key to making sense of the star-nosed mole is the habitat where the animal lives, wetlands. In this environment they compete with other animals, especially shrews, for food, so having a prey category to themselves would be especially useful. The star likely evolved as a means to better find and handle small prey quickly.

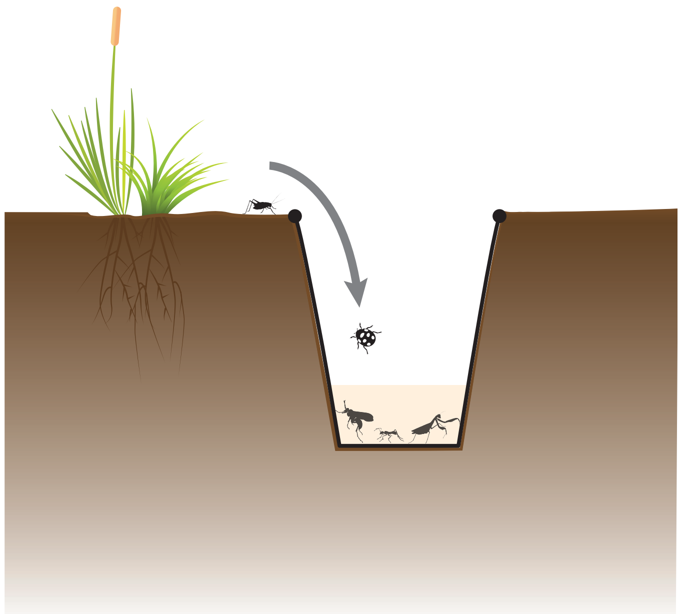
Star-nosed mole pups showing the star nose. (HIL)



Several animals have a strict relationship with soil as they build their nests in it or use it as a hunting-ground. (**a**) Armadillos (family Dasypodidae) and (**b**) the burrowing owl (*Athene cunicularia*) are two good examples. (DC, MK)

Methods to study soil biodiversity

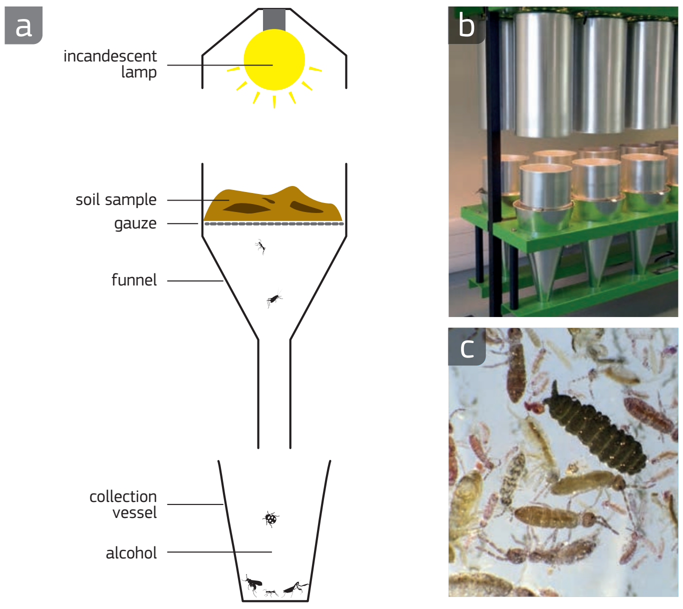
The enormous diversity of soil biota, in terms of size, number and characteristics, means that there is a concomitantly large range of techniques required in order to collect and, subsequently, identify the constituent organisms. Collection necessarily involves the separation of the organism from the soil matrix, which can be challenging due to the nature of soil minerals and organic constituents, and the physical nature of the soil matrix. Many prokaryotes (see pages 32-35) are strongly adhered to soil particles, and their release can be achieved by physical disruption (e.g. grinding and sonication) or the addition of specific chemical agents (e.g. surfactants and chelants). Such disruption can lead to damage of the organisms and, therefore, there is always a compromise between disturbance and eventual detection. The substantial differences in density between soil mineral constituents and organisms offers a means of separation by elutriation, centrifugation or density gradients. Motile and mobile organisms can be collected by encouraging movement away from the soil matrix, to entrapment and collection vessels, by a combination of gravity and differential application of heat or light. For example, the Tullgren funnel is an apparatus used to extract living organisms, particularly arthropods, from samples of soil, while the Baermann funnel is used for extraction of nematodes from soil. The active surface-dwelling mobile mesofauna, such as collembolans and mites (see pages 49-50), can be collected by possibly the simplest of all devices: the pitfall trap, which consists of a pot buried in the soil such that the lip is contiguous to the soil surface and fauna fall into it during their passages. The physical form of any organism, whether a single microbial cell or a large animal, is termed the 'phenotype', which is formally defined as the interaction between the genetic makeup ('genotype') of an organism and the environment in which it has developed and now lives. Historically, identification of soil organisms was predominantly reliant on visual observation, and thus based on the way they appeared (i.e. their morphology). Now biochemical approaches are being increasingly used, primarily based on DNA analyses (see box on page 30). [76, 77]



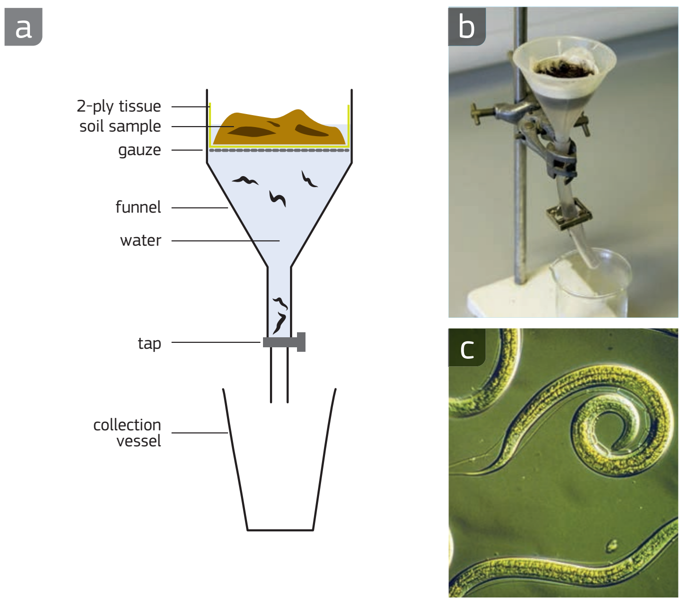
Schematic of a pitfall trap used to collect mobile, active soil mesofauna, such as mites and collembolans, and macroarthropods. (KR)

From morphology to biochemistry

Soil prokaryotes (archaea and bacteria) (although notably a tiny proportion of the total) and many fungi (see pages 38-41) form characteristic colonies when grown in laboratory conditions (*in vitro*) on enrichment media, which can be used as diagnostic for identification. More visually anonymous forms were often identified on the basis of their distinct enzyme profiles or ability to utilise particular combinations of substrates, but these techniques are now generally archaic, superseded by nucleic acid analysis. There is a long heritage of identification of soil micro-, meso- and macrofauna based on morphological features, but these can be remarkably subtle and require considerable experience and expertise to carry out. The traditional taxonomic tools of microscopes and systematic keys (written, structured identification protocols) are gradually being supplanted by genetic analysis of DNA derived from the organisms, notwithstanding that such approaches currently require advanced laboratory equipment.

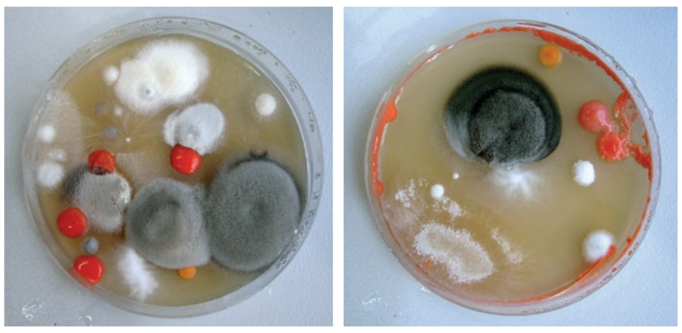


(**a**) Schematic of a Tullgren funnel for extraction of arthropods from soil samples. Heat and light from the lamp drives fauna downward such that they fall through gauze and into preservative liquid. (**b**) Example of professionally made funnel array. (**c**) Example of faunal community extracted from grassland soil using this technique. (KR, FEC)



(**a**) Schematic of Baermann funnel for extraction of nematodes from soil samples. Nematodes migrate downwards with gravity and through a gauze layer, then sink to the base of the funnel spout. The collection is completed by opening the tap. (**b**) Example of apparatus. (**c**) Example of grassland soil nematode community extracted using this technique. (KR, CSIRO)

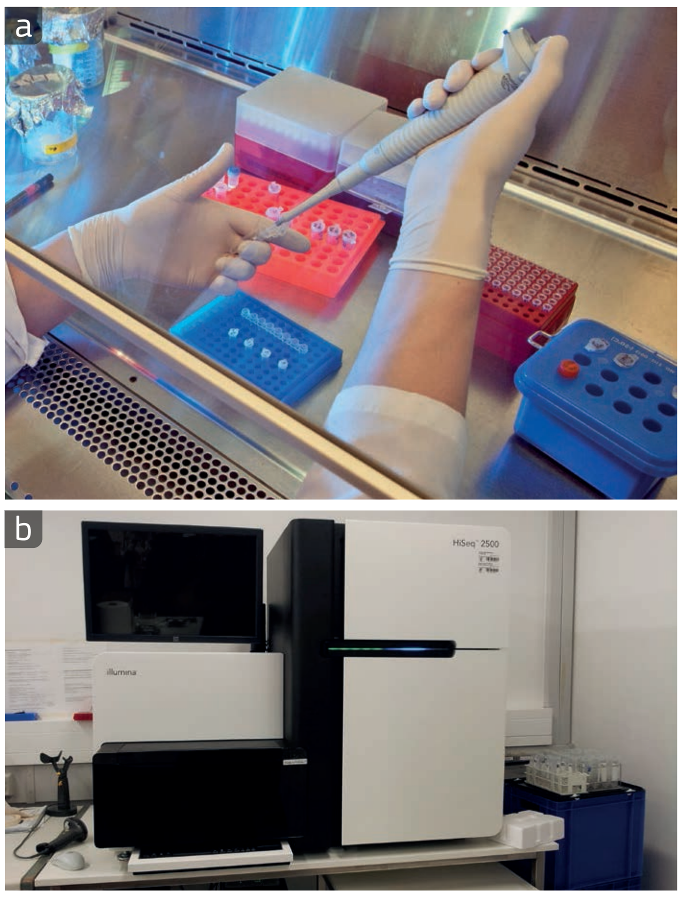
These techniques are becoming increasingly refined and accurate as the range and extent of gene sequences of soil biota become more widely available. Genotyping and phenotyping concepts can also be applied at a whole-community scale as well as to individual organisms. The concept can be useful in describing soil communities due to their inherent enormous complexity, and due to the fact that several of the key functions delivered by the biota, such as carbon mineralisation or soil structural dynamics, arise not from the action of particular species, but at a community scale. For example, knowing the precise identity of each of several thousand million bacteria might not be useful in terms of informing about soil respiration or porosity, but there are higher-order relationships between the whole community structure and the delivery of such functions. Application of the 'community phenotype' concept, particularly in relation to the biochemical composition of lipids found in cell membranes ,is becoming common. This is because there appears to be a high degree of consistency in such profiles in relation to the environmental circumstances of a soil, and they are sensitive to environmental change, and can be used as indicators of broad organismal groups, such as some bacteria or fungi.



Morphologically diverse bacterial and fungal colonies derived from soil, growing in the laboratory (*in vitro*) in Petri dishes. Under the microscope, it is possible to identify bacteria and fungi on the basis of colours, shapes and other morphological features. However, this method is highly unrepresentative of the majority of soil microbial life. (JA)

Soil DNA and RNA

DNA and RNA can either be extracted directly from soil or from organisms previously separated from soil. Extracted DNA must be purified to avoid interference of organic compounds, particularly humic acids, which are prevalent in many soils. Resultant DNA mixtures should be representative of the entire basal community structure, known as the 'metagenome', while RNA is associated with nominally active organisms, since this is related to particular forms of DNA being transcribed and, therefore, is known as the 'metatranscriptome'. There are a number of ways to analyse resultant nucleic acids, from a very broad taxonomic scale to extremely precise determinations of particular species. Rapid advances in technology are revolutionising the scale of such analyses and the throughput that can be attained. It is now feasible to obtain several million sequences in a metagenome analysis of a single soil community sample, and these can then be attributed to their taxonomic origins and allow remarkably detailed descriptions of community structures. Emergent next-generation systems (see box on page 157) will enable thousand millions of sequences to be determined with relative ease, leading to what are likely to be entirely new perspectives on how soil microbial communities are structured and how they function. The incisive analysis and interpretation of such huge datasets is very challenging and also drives new developments in informatics relating to such 'Big Data'.



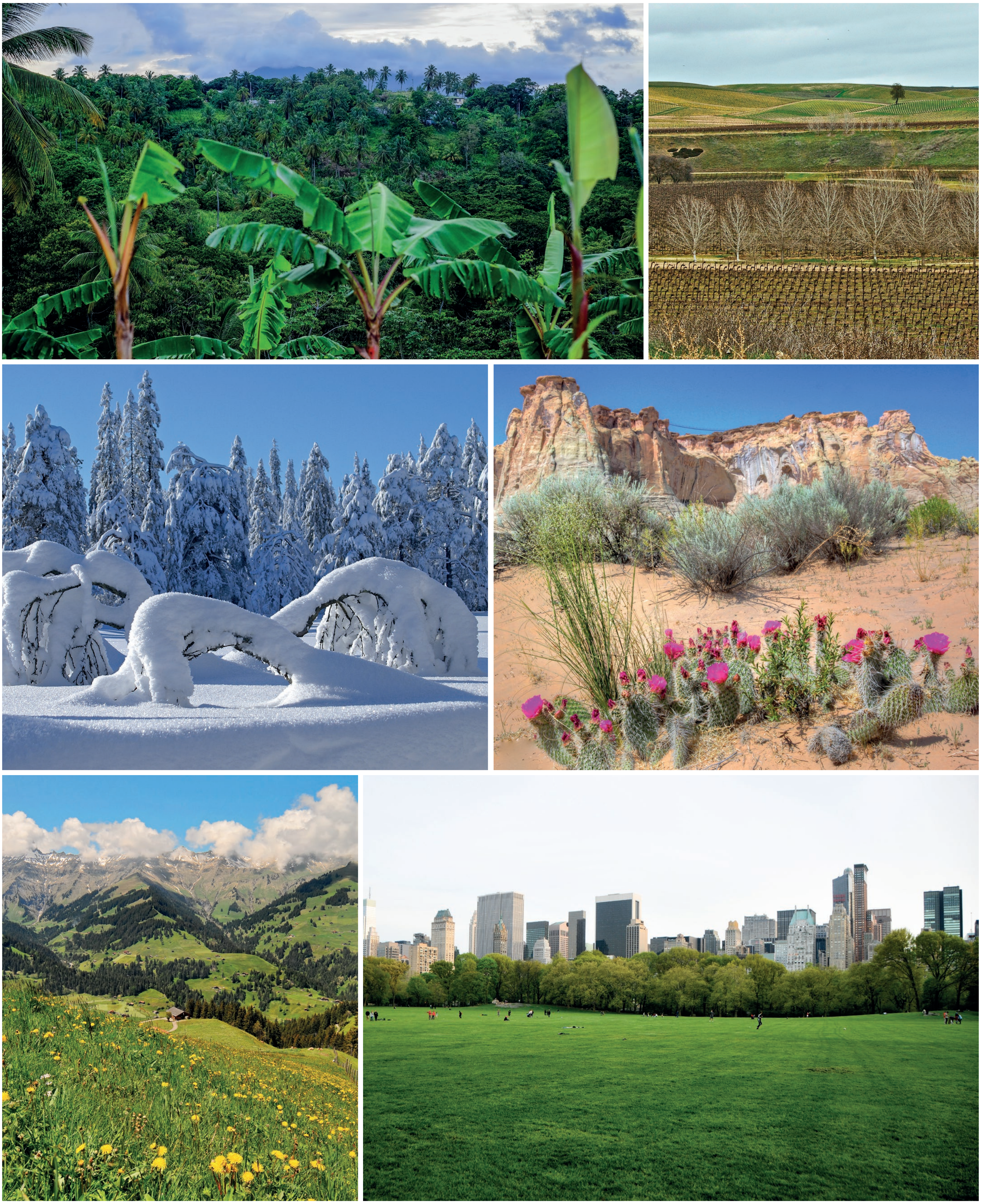
(**a**) A researcher working on DNA in a laboratory. (**b**) One of the high technology instruments currently used to sequence DNA. (UMS, KF)

Sampling design

- If the identification and/or quantification of target groups of soil organisms is necessary, appropriately organised sampling designs are required.
- The aim is to acquire a collection of samples of the target group that are sufficiently representative of the area or ecosystem under consideration.
- Statistically robust sampling is necessary, since it allows an estimation of the likely variation in any metrics and, consequently, how accurate they are. A wide range of statistical sampling strategies can be prescribed, depending on specific aims. These include designs that can target broad general estimations, or those that focus principally on characterising the spatial patterning or temporal variation of the target groups.
- Where techniques are laborious, sample sizes can be restricted. High-throughput molecular-based techniques are significantly reducing such restrictions, and offering new opportunities in understanding how soil communities are organised in time and space across a wide range of scales.
- Sampling of the soil biota is typically based on *ex situ* and *in situ* techniques. The former involve removing prescribed volumes of soil, by coring or excavation, and generally transporting them back to the laboratory for assay. *In situ* techniques involve procedures applied in the field, and generally rely on the movement of the organism(s) to a collecting device.

Summary of collection and identification approaches of the main groups of soil organisms

Main division	Group	Extraction/collection techniques *Based on sub-samples of soil taken from the field unless otherwise stated*	Identification	Notes
Entire community	Whole community phenotype	Extraction of indicator biomolecules from entire soil samples, usually involving organic solvents, such as methanol or hexane	Chemical structure of constituent molecules	The most pervasive approaches are based on membrane lipids such as phospholipid fatty acids (PLFAs) and neutral lipid fatty acids (NLFAs). The caveat is that relationships between fatty acid composition and taxonomic status is somewhat diffuse. Respiratory quinones can also be characteristic. Generic structural molecules such as ergosterol (fungi) or chitin (insects, arachnids) can only serve as surrogates for total biomass and are not useful in terms of identification. Extent of 'community' is essentially defined operationally by sieve size through which the soil sample is passed prior to extraction
Prokaryotes	Bacteria and archaea	Enrichment cultivation in liquid or on semi-solid media	Morphology of colonies and constituent cells, physiological profiling (now archaic), nucleic acid analysis	Colonies – strictly, 'colony forming units', CFUs – assumed to develop from individual cells. Thus underestimation can occur where aggregations of cells are not completely developed. Only 0.1 - 1 % of prokaryotes confirmed as being extant in soil (via analysis of community DNA) are apparently expressed in enrichment culture systems. Representivity for community-scale profiling is therefore questionable, but the technique can be applicable in appropriate circumstances
		Direct extraction from soil matrices via density-gradient centrifugation	Nucleic acid analysis	Cells must be released from any attachment to soil particles; otherwise density-based discrimination will not operate. Extraction efficiency is accordingly variable, and always less than complete
		Extraction of nucleic acids from extracted cell suspensions or directly from soil samples		'Whole community DNA'. See 'Soil DNA and RNA'
Protists	Ciliates, flagellates, amoebae, etc.	Enrichment culture in liquid media	Morphology, nucleic acid analysis	Quantification based on most-probable-number (MPN) techniques involving dilution-to-extinction approaches
		Direct extraction from soil matrices via density-gradient centrifugation		Protection from osmotic shock needed, can be achieved by pre-treatment of soil samples with fixatives
Fungi	Fungi: generic soil	Enrichment cultivation in liquid or on semi-solid media	Morphology of spores (especially), mycelia and hyphae. Can be supplemented by DNA analysis	CFUs can arise from spores or mycelial fragments – hence number apparent will be a function of intrinsic spore numbers and mycelial mass but modulated by the extent of spore cluster dispersal; degree of (and propensity to) mycelial fragmentation; disruption of such hyphal fragments; and complex interactions in the media between emergent colonies. Hence 'enumeration' of fungi ostensibly in the soil system via CFUs should be treated with due caution
		In situ trapping of active mycelia via their incursion into buried 'ingrowth' meshes/ tubes	Trapped specimens grown-on via media, identified as above	
		Extraction of nucleic acids directly from soil	Nucleic acid analysis	'Whole community DNA'. See 'Soil DNA ansd RNA'
		Fruiting body collection	Morphology of fruit body and associated spores	Typically most relevant to aboveground manifestation of such structures from Basidiomycetes and Ascomycetes, where they are sufficiently large to be visible to the unaided eye. Relationship to belowground fungal flora and any associated mycelial extent can be tenuous
	Fungi: mycorrhizal	Based on sampling of host roots, via extraction by washing from soil cores, or direct excavation from the field. Spores can also be extracted from dispersed soil by washing and filtration, elutriation or microscope-aided hand-picking	Morphology of mutualistic structures, morphology of spores (especially arbuscular forms), nucleic acid analysis	
		Fruiting body collection	Morphology of fruit body and associated spores	As for fungi (generic soil) – see above
Microfauna	Nematodes	Wet extraction by migration-based filtration through coarse tissue to collection vessels ('Baermann funnels')	Morphology, especially of mouthparts, nucleic acid analysis	Cysts not detected, relies on movement by active individuals, so can be selective
		Direct wet extraction by elutriation and capture on sieves		Cysts and inactive forms may be detected
		Density gradient cushions or centrifugation		
	Tardigrades	Wet extraction by migration-based filtration through fine mesh to collection vessels, or direct observation via dissecting microscope and physical removal		
	Rotifera	Wet extraction by migration-based filtration through fine mesh to collection vessels, using differential temperature gradient		
Mesofauna	Legged forms	Dry extraction by light and heat-induced migration to collection vessel ('Tullgren funnel')	Morphology, nucleic acid analysis (emergent)	
		In situ collection of active (foraging) forms via pitfall traps		If predators are present in traps, they can consume co-collected prey, leading to underestimation of the latter. If non-living specimens are acceptable, biocides, such as alcohol or polyethylene glycol solution, can be placed in the bottom of traps
	Enchytraeid worms and Diptera larvae	Wet extraction by migration-based filtration through fine mesh to collection vessels (akin to Baermann funnels – see nematodes above)	Morphology	Only active forms extracted due to reliance on movement to separate them
		Elutriation		
Macrofauna	Earthworms	Excavation of defined volumes of soil and hand-sorting	Morphology	Laborious technique, can involve substantial masses of soil
		In situ expulsion from soil matrix via addition of expellants such as mustard solution or formaldehyde		Efficiency relies on pervasive penetration of the soil matrix by expellant solution, since contact with worm is needed to encourage upward migration. Not all worms affected will take this path. Formaldehyde is now discouraged due to potential environmental side effects and health and safety issues
		Electromigration to surface via application of pulsed high voltage, delivered to soil via inserted electrodes in an annular pattern		Affected by soil type and prevailing moisture. There could be health and safety issues due to high voltages involved
	Other macrofauna	Hand-picking; pitfall trapping; direct observation		
Megafauna	General	Hand-picking; trapping; direct observation, including remotely by videography	Morphology	



From tropical forests and grasslands to cold and hot deserts, agricultural fields and also city parks, soil organisms can be found in every ecosystem on our planet. Soil biodiversity is distributed not only through space, but also over time (i.e. days, seasons and years). (MRI, LTA, RHU, SJR, GK, TTJ)

Introduction

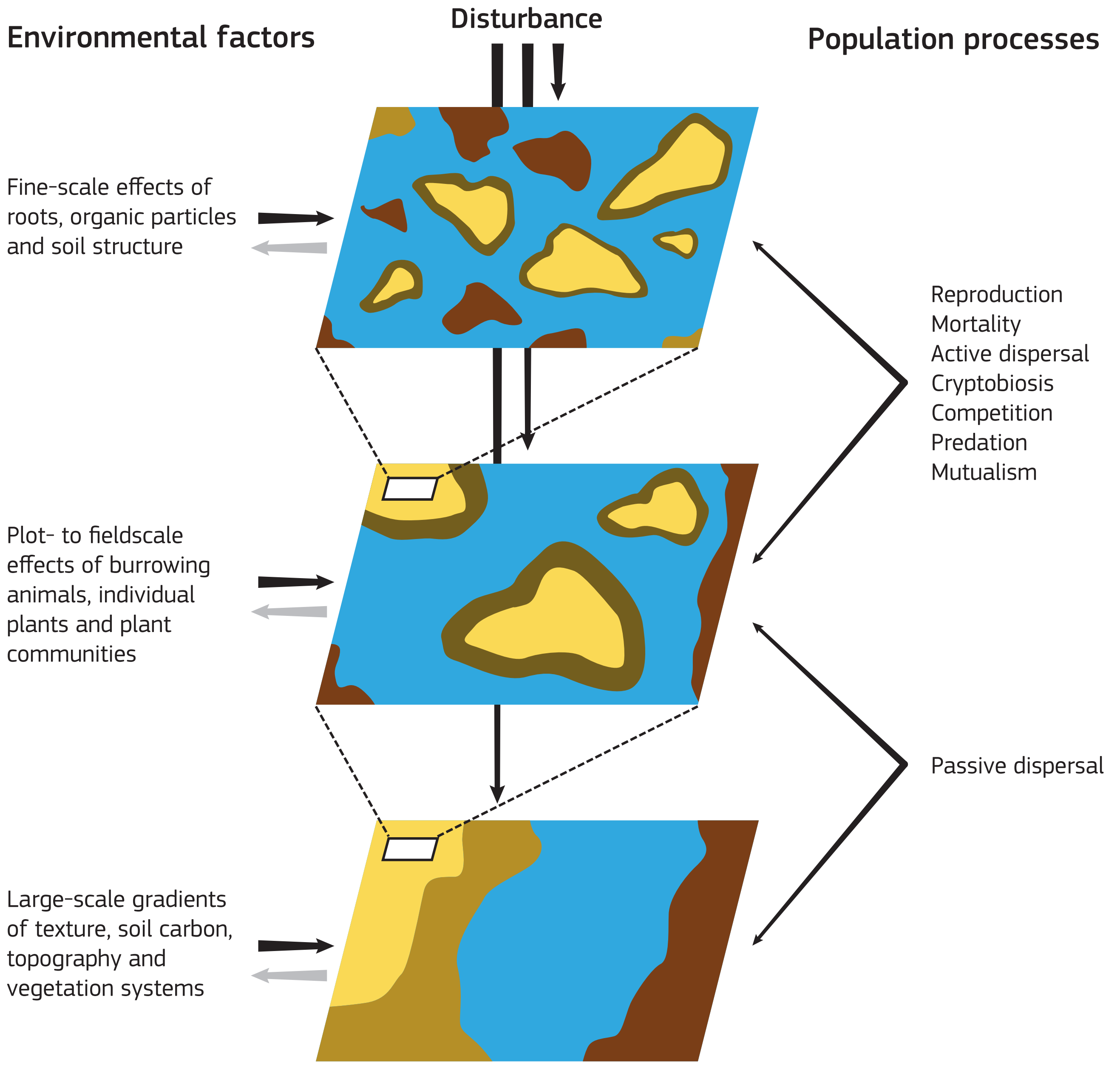
Soils are among the most diverse habitats on Earth, and determination of the forces that operate at different scales that drive this diversity is one of the greatest challenges in soil ecology. Environmental factors work at the local scale of organic particles and plant roots, but also at the level of plant communities and, at more regional scales, related to topography and vegetation systems. Disturbance operates at all these scales and is an important factor for maintaining a high degree of habitat diversity in soil. Limitations in the dispersal of organisms through the soil matrix, and heterogeneous distribution of resources, make the majority of soil particle surfaces devoid of organisms when observed under a microscope. This restricts population processes, such as competition, to local hotspots with high resource availability. Therefore, organisms that normally compete, can coexist by being spatially separated. Many soil organisms utilise similar resources in the soil and there is an apparent contradiction between the high species richness and the low degree of resource specialisation. This high level of coexistence among species in the soil (33 000 bacterial and archaeal taxa can be detected in less than 10 grammes of soil) can only be understood when realising the exceptionally large degree of spatial heterogeneity and microhabitat diversity in the soil. Soil may appear rather homogeneous when viewed on a large scale, but becomes more and more heterogeneous when approaching the scale of individual organisms.

Many soil organisms operate at the level of aggregated particles, and the stability of these aggregates are important when three-dimensional networks of water and air-filled pores are formed in the soil. Recent work using scanners has demonstrated a spatial distribution of potential microbial resources (e.g. polysaccharides, proteins, etc.) at the nanometre scale in microaggregates (10–100 µm in size), demonstrating an enormous spatial complexity which helps explain the high microbial diversity of soils. Soil microbes contribute to this complexity by producing fungal hyphae and sticky substances (e.g. exopolysaccharides, glomalin), that bind organic and mineral particles together into aggregates.

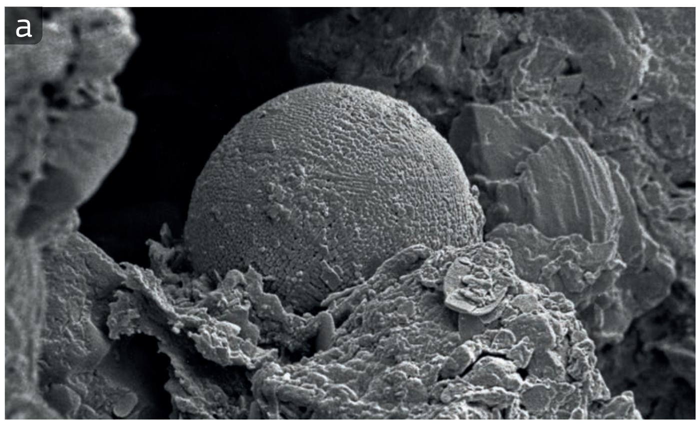
Certain properties (e.g. soil structure) influence plant distribution, and the activity of plants are important in shaping soil communities. For instance, substances exuded by roots result in high microbial activity at the root surface (the rhizosphere effect) and such gradients of resources (nutrients, aeration, redox potential) in soils can be steep and change rapidly over time. Other environmental factors work on much longer time scales (e.g. plant successions). Variation in litter quality and exudation patterns among plants also influence soil organisms, and spatial patterns of soil communities are often reflected in spatial plant distribution patterns. The activity of soil communities can also shape plant communities. For instance, macrofauna, such as termites or ants, redistribute resources, such as organic matter, in the landscape, which has profound effects on vegetation patterns.

Abiotic drivers, such as climate, pH and soil moisture, are often important factors in shaping soil communities on larger scales, but plant functional traits may also be important. For instance, fast-growing plant communities are usually associated with soil microbial communities that are dominated by bacteria, while fungi dominate in soils of slow-growing plant communities. On continental scales, pH is one of the most important factors shaping soil microbial communities, and this factor alone explains most of the variation in microbial soil communities, ranging from tropical forests and grasslands to temperate and boreal forests.

The aim of this chapter is to present the biotic and abiotic factors that influence the spatial and temporal patterns of soil communities, and to give an overview of the global distribution of soil biodiversity on the basis of current scientific knowledge.



Spatial distribution of soil organisms is influenced by many environmental factors that act from small to large scales. Disturbance operates at all spatial scales and can be a key driver, for example through the alteration of the physical structure of soil. Interactions (dotted arrows) between the spatial distribution of soil biodiversity and environmental factors add further complexity to the system. Soil organism features, such as body size, dispersal mechanisms and life-history characteristics further influence the population and processes carried out by soil organisms. The field of science that studies all this complexity is known as spatial soil ecology (derived from Ettema and Wardle, Trends in Ecology & Evolution, 2002). [78]



Soil biodiversity ranges from the micro- to global scale, from (**a**) a scanning electron micrograph of a fungal spore in the soil matrix to (**b**) a whole ecosystem, such as this boreal forest in Sweden. (TEI, ABA)

Distribution patterns – Biogeography

Historical and scientific context

Biogeography is the study of the large-scale distribution of biodiversity through space and time. This science aims to reveal biodiversity regulation and its link with ecosystem biological functioning, goods and services, such as maintenance of productivity, of soil and atmospheric quality and of soil health. Although the initial concept dates back to the early 20th century, only recently an increasing number of studies have investigated the biogeographical patterns of soil organisms. This delay is due to the lack of relevant molecular and bioinformatics tools (see pages 64-65) to assess the scale and inaccessibility of soil biodiversity, and the non-availability of an adequate sampling strategy. [79, 80]

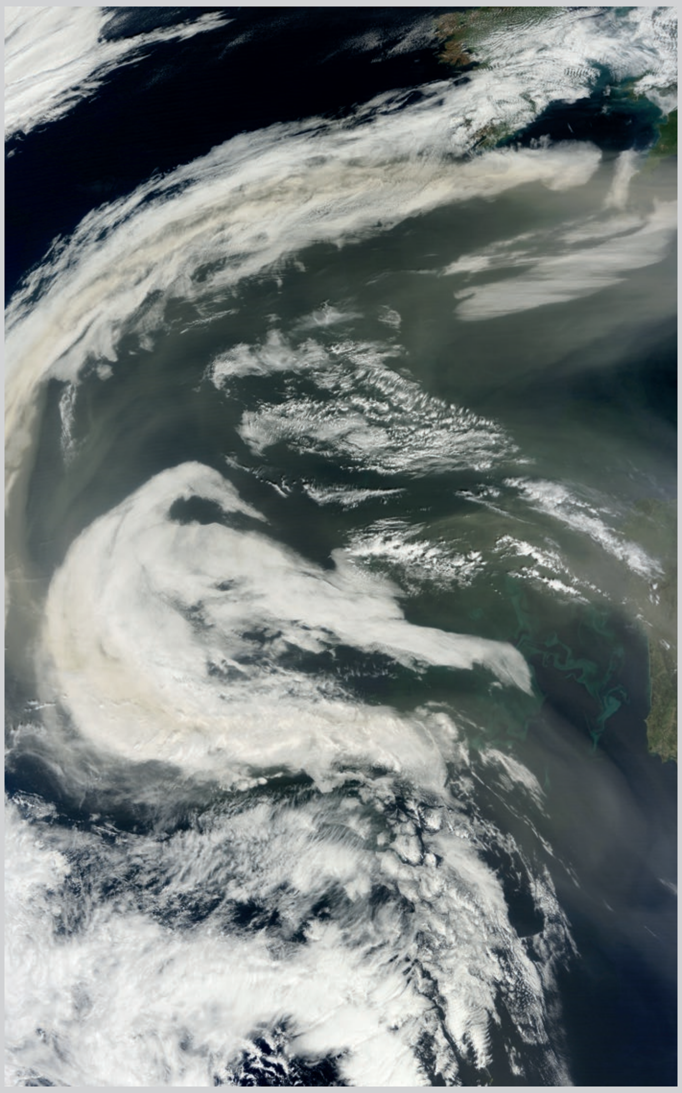
Ecologists studying plants and animals have long recognised that an examination of the modifications in diversity throughout a landscape is pivotal to understanding the environmental factors that drive the magnitude and variability of that diversity. However, this conceptual vision is also relevant to soil life since it can offer valuable insights into the relative influence of dispersal limitations, environmental heterogeneity, and environmental and evolutionary changes in shaping the structure of communities. Soil biodiversity is extremely complex, ranging from microorganisms (e.g. bacteria) to macrofauna (e.g. earthworms). As a consequence, the question to address is whether the same laws govern the distribution of soil micro- and macroorganisms or whether some peculiarities (e.g. minute size, short generation time, huge diversity and high dispersal and adaptation of microbial communities) lead to specific patterns of distribution on large spatial scales. To date, the studies dealing with the biogeography of the soil community allow us to answer some of the questions that arise when considering large scales:

- are soil communities a 'black box' with no spatial structure or do they exhibit a particular distribution with predictable, aggregated patterns on local to regional scales?
- are spatial variations brought about by contemporary environmental factors or historical land use and contingencies?
- which environmental factors (e.g. soil properties, climate, land-use and human disturbance) contribute most to the structure and diversity of the soil community on large geographic scales?

Is everything everywhere?

- Plants and animals have long been demonstrated to be distributed in biogeographical patterns corresponding to the heterogeneous distribution of their diversity through space and time.
- These patterns have been related to ecological processes that shape community diversity: environmental selection, speciation, drift and dispersal (the movement and successful establishment of an individual from one location to another through passive or active mechanisms).
- Because microorganisms are small and easily transported (e.g. by wind and water), it has long been considered that soil microbial communities were not dispersal limited, supporting the postulate 'Everything is everywhere, but the environment selects'. [81]
- This is known as Baas-Becking's postulate, from Lourens Baas Becking, a Dutch botanist and microbiologist who made this statement. Under this postulate, the biogeographical patterns demonstrated for soil microbial communities would be only determined by environmental selection, and identical environmental conditions would lead to identical composition of microbial communities.
- In a recent study, soil bacterial community composition at the scale of the size of France was characterised by means of molecular analysis. Based on this characterisation, researchers estimated the soil bacterial community composition in sites at increasing distance from one another. Also, researchers found a relationship between soil bacterial communities and soil habitats (based on soil physical and chemical characteristics and land-use) with increasing distance.
- This strong relationship was in agreement with the strong dependency of soil bacterial community composition on soil habitat characteristics.
- Nevertheless, the composition of two soil bacterial communities could differ in fully homogeneous environments. This observation contradicts the Baas-Becking's postulate for soil microorganisms.
- Therefore, despite their small size and supposed high dispersal abilities, every soil microorganism may not be everywhere, and future massive inventories of soil microbial diversity may support this hypothesis.

Gone with the wind



A very large cloud of beige dust floating over the Atlantic Ocean off the shores of western Europe. The dust originated from the Sahara desert in North Africa, stirred by strong winds that are likely carrying millions of microorganisms. (NASA/GSFC/JS)

- During the great age of natural history exploration in the 19th century, it became abundantly clear that many animal species, especially the larger ones, had restricted geographical distributions.
- The microbiologist Martinus Beijerinck and his pioneering studies showed that diverse types of bacteria could be cultured from almost any type of natural material, and species recorded from a particular habitat type located in geographically distant places were usually similar, if not identical to each other.
- Many forces in the natural environment drive the dispersal of small organisms (e.g. wind, hurricanes and global oceanic circulation).
- Microorganisms are abundant in the upper atmosphere, particularly downwind of arid regions, where winds can mobilise large amounts of topsoil and dust. [82]
- In the atmosphere, densities of bacterial cells typically exceed 1×10^4 per cubic metre.
- In the atmosphere, it is possible to find not only bacteria but also microbial eukaryotes, such as some groups of protists (see pages 36-37).
- Numerous studies have suggested that the presence of microorganisms in the atmosphere may impact cloud development and microbial biogeography.
- The dispersal through the air is a pathway for rapid long-distance dispersal of microbes, allowing some species to overcome geographic barriers.
- The efficiency and randomness of airborne dispersal is an important factor in determining whether evolutionary history and chance events play a role in the distribution of taxa.
- Bacteria enter the atmosphere in aerosol particles from practically all surfaces, including soil, water and vegetation. Once airborne, they are carried upwards by air currents and may remain in the atmosphere for many days before being removed by precipitation or direct deposition onto surfaces.
- Meteorological variables, especially temperature and wind speed, are known to affect the atmospheric concentrations of microorganisms.
- The study of possible effects of wind on the biogeography of soil microorganisms is not easy since the collection of living samples from the upper atmosphere is extremely challenging.

Frontispiece to Alfred Russel Wallace's book *The Geographical Distribution of Animals.* Alfred Russel Wallace is commonly known as the father of biogeography after his contributions regarding the distribution of organisms. (DYS)

Drivers of soil biodiversity distribution

The factors that regulate the diversity and distribution of belowground communities are less understood than those acting on aboveground organisms. The activity and diversity of soil organisms are regulated by both abiotic and biotic factors. The main abiotic factors are climate (temperature and moisture), soil texture and structure, salinity and pH. Overall, activity and growth of soil organisms increase at higher temperatures and soil moisture levels. For instance, for collembolans (see page 50), the optimum average temperature is 20-50 °C, while some bacteria (see pages 33-35) can survive temperatures up to 100 °C.

Soil texture and structure also strongly influence the activity of soil biota. For example, clay soils favour microbial and earthworm (see page 58) activities; whereas sandy soils, with lower water retention potential, are less favourable. Soil salinity can also cause severe stress to soil organisms, leading to rapid desiccation. However, increased salinity may sometimes have positive effects, by making more organic matter available. Similarly, changes in soil pH can affect the activity of species and nutrient availability. The main biotic factors are vegetation composition and diversity, and aboveground trophic interactions. In addition, within soil food webs (see page 96), each group can be controlled by bottom-up or top-down interactions. Top-down effects are mainly driven by predation, grazing and symbiotic relationships (see box on page 33). Bottom-up effects depend largely on competition for access to resources.

Recent biogeographical studies on soil communities have mainly focused their attention on microbial communities; in particular, on the distribution of soil bacteria (see pages 33-35). However, as described in this chapter, information on factors influencing the distribution of other groups of soil organisms are increasingly studied and understood. Nevertheless, it will be important to conduct new studies in order to improve the robustness of our results and, therefore, our understanding of soil community biogeography. The following are suggestions for future investigations:

- conduct more extensive soil sampling strategies targeting large-scale territories, including very diverse environmental characteristics in terms of soils, climate and geomorphology
- investige more than the rudimentary mapping of soil organism diversity, in order to deduce significant biogeographical patterns
- apply statistical techniques and modelling to robustly rank the environmental filters that structure these patterns
- distinguish the environmental filters that structure the spatial distribution of the community as a whole, but also the major and minor populations that constitute such communities

Extensive sampling of soil organisms is needed to allow precise descriptions of soil biodiversity distribution at a large scale. (AO)

Distribution patterns – Distribution of soil organisms

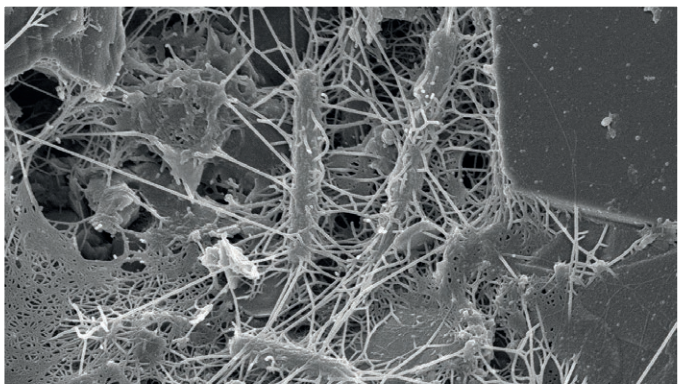
Distribution of soil microbial communities

Microbial ecologists describing the distribution of soil microorganisms (e.g. bacteria and fungi – see pages 33-35, 38-41) on a large spatial scale generally invoke one of the oldest fundamental paradigms in microbial ecology 'everything is everywhere, but, the environment selects' (see box on previous page). The first part of this paradigm, 'everything is everywhere', is supported by several particularities of the microbial model: microorganisms 1) are small and easily transported; 2) have the ability to form a resistant physiological stage that allows them to survive in hostile environments, and 3) form extremely large populations with a high probability of dispersal and a low probability of local extinction. [83, 84]

The fact that more than a trillion (10^{18}) microorganisms are transported annually through the atmosphere (see box on previous page) between continents supports the hypothesis of a wide dispersion of microbes. Bacteria can also be isolated from places where 'they should not be', such as thermophilic bacteria from cold seawater. By contrast, the second part of the paradigm, 'the environment selects', suggests that different microbial assemblages are maintained locally according to environmental variations. This challenges the 'everything is everywhere' tenet, which claims that microbial communities are homogeneous, whereas the second part of the paradigm leads to microbial differentiation between habitats or locations. Altogether, the available studies dealing with the biogeography of soil microbial communities have demonstrated several significant findings, such as:

- a significant but moderate diversification of microbial communities on a large scale
- a hierarchy in the influence of environmental parameters with a strong influence of soil characteristics (notably pH) and also types of soil use
- a weak influence of climatic and geomorphological (i.e. surface features of the Earth) parameters on the composition of communities, and a total independence of the composition of such communities with regard to the geographical distance separating them

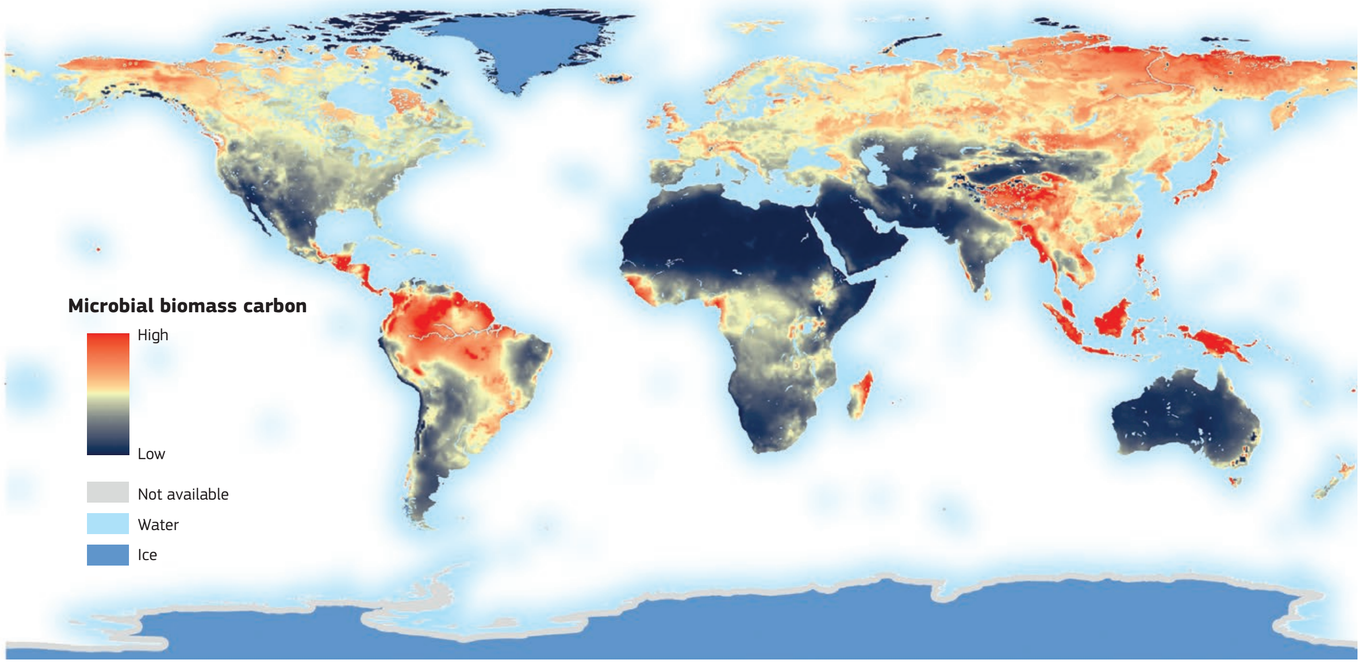
Most of these studies compare soil microbial diversity and composition in very different types of ecosystems (generally chosen *a priori*) that facilitate the discrimination of communities and intensify the relationship with contrasted environmental filters (e.g. soil type, climatic conditions, land cover, etc.). However, in certain cases the reduced soil sampling methodology (less than 100 sites) can lead to contradictory results given, for example, the influence of climatic conditions on soil bacterial diversity. To date, it is impossible to come to sound conclusions about the rank of environmental filters driving the soil microbial assembly to a large extent.



Bacteria in soil. A gramme of soil can contain millions of bacterial cells. (ADO)

Soil bacterial communities

Bacteria are by far the most abundant organisms in soils, with several thousand million cells present in a single gramme of most soils. Bacteria play important roles in the plant-soil system; firstly, by both fixing and transforming nutrients (see page 106) vital to other organisms, but also by influencing the overall ecology of the system through positive or negative biotic interactions with other organisms. They are able to grow rapidly and, therefore, can adapt rapidly to environmental change. This ability causes many issues in precisely defining what represents a bacterial 'species'. However, it is known that bacteria are genetically diverse (i.e. belong to different species) despite only exhibiting a limited number of visible morphological differences. The complex physical structure of soils allows many different spatial niches for this diversity to flourish, and for this reason soils are known to be one of the most biodiverse habitats of bacterial communities.



Global estimates of soil microbial abundance. Patterns depict soil profile microbial biomass in terms of carbon estimated as grammes per square metre (derived from Serna-Chavez *et al.*, Global Ecology and Biogeography, 2013). (JRC) [85]

New data, new knowledge

In the past, our knowledge of the different types of bacteria found in soil, and the factors affecting their distributions, has been limited to findings from the analyses of culturable bacteria that can grow on nutrient-rich media in the laboratory (see pages 64-65). These findings are now being complemented by data from large-scale soil surveys using molecular techniques to assess biodiversity.

The molecular approaches typically rely on the determination of bacterial biodiversity by examining sequence differences in DNA that has been extracted from the soil. These new approaches are vastly increasing our knowledge of the different types of bacteria found in different biomes around the world, revealing entire lineages of bacterial life for which no living cultured representative species have been isolated. Molecular surveys of soil have typically been performed to understand how natural factors influence the distribution of biodiversity, but also to reveal how sensitive these bacterial communities and their functions are to environmental change resulting from, for example, human land usage and climatic variations.

Drivers of soil bacterial diversity

A striking consistency in the many large-scale studies that have been performed is the overriding influence of soil properties on soil bacterial communities. Across landscape gradients, from upland bogs and woodlands through grasslands to intensive lowland arable systems, predictable changes occur in the broad taxonomic makeup of bacterial communities which can be related to changes in soil properties, such as acidity and organic matter content. Acidic habitats, such as upland bogs or lowland heath, with characteristic high levels of organic matter resulting from low decomposition, are characterised by relatively low biodiversity. This biodiversity is made up of many previously undiscovered taxa, such as the acidobacteria, which are specialised for living in such physiologically harsh environments. In more neutral habitats, like those favoured for agriculture, there are more diverse assemblages of bacteria, that are better-known due to culture-based studies (e.g. actinobacteria – see page 35). Certain bacterial groups, such as the alphaproteobacteria, are ubiquitous (occurring everywhere). Their ubiquity most likely points to a potentially large role that these organisms play in maintaining soil processes.

Soil bacterial communities are also driven by other factors. These are the same forces that affect soil formation itself: climate, parent material, topography and interactions with other organisms (see Chapter I). For instance, plant diversity is of course a key driver in the long term, as it provides the important raw detrital materials on which the microbial communities build the soil. In the short term, plants provide labile exudates from their roots (see page 43), which feed the bacterial activities and the local diversity of communities. It is difficult, perhaps even impossible, to determine the relative importance of each of the different factors in driving soil biodiversity, because of their inherent interdependencies. However, because of the increasing demand for food production, one factor that is heavily altered by human populations is the plant communities. For this reason, there is a heightened interest in plant and agronomic effects on soil bacterial biodiversity. More modern advances in molecular sciences are now used to address these issues.

The recognition and understanding of how and why different soils possess different bacterial communities will allow the development of a better ecological framework for future testing of how global changes will affect bacterial communities.

A scientist (**a**) measuring soil pH and (**b**) showing soil rich in organic matter. Organic matter content and pH are some of the most important drivers shaping soil microbial communities from bogs, woodlands through grasslands to intensive arable systems. (IF/CIFOR, CKE/NRCS)

Distribution patterns – Distribution of soil organisms

Soil fungal distribution

The kingdom Fungi is one of the most diverse groups of organisms on Earth, which are important actors for the regulation of carbon cycling, plant nutrition and pathology (see Chapter IV). Fungi are widely distributed in all terrestrial ecosystems. A study published in 2014 determined the main drivers of fungal diversity and community composition globally. To investigate soil fungal diversity, researchers used DNA (see page 64-65) extracted from hundreds of globally distributed soil samples. The strongest drivers on the richness (or diversity) of fungi are proximity to the Equator and mean annual precipitation. Higher levels of diversity were found in tropical ecosystems. However, ectomycorrhizal fungi (see page 40) were most diverse in temperate or boreal ecosystems. Precipitation and temperature (climatic factors), followed by pH, calcium or phosphorus availability (edaphic factors), are the most significant drivers of soil fungal richness and community composition at the global scale. Strong links found among distant continents reflect their relatively efficient long-distance dispersal (through wind and water) compared with that of large animals.

Another recent study investigated the intensity at a global scale of the colonisation of plant roots by the two main types of mycorrhizal fungi: arbuscular and ectomycorrhizal fungi. The intensity of plant root colonisation by arbuscular mycorrhizal fungi strongly relates to warm-season temperatures, frost periods and the soil carbon-to-nitrogen ratio, and is highest at sites featuring continental climates with mild summers and a high availability of soil nitrogen. By contrast, the intensity of ectomycorrhizal infection in plant roots is related to soil acidity, the soil carbon-to-nitrogen ratio and the seasonality of precipitation, and is highest in sites with acidic soils and relatively constant precipitation levels. Both studies prove the good level of knowledge of the factors determining the distribution of soil fungi at the global scale. Information about the forces driving the spatial patterns are available not only for soil microorganisms (e.g. bacteria and fungi), but also for soil microfauna, namely nematodes.

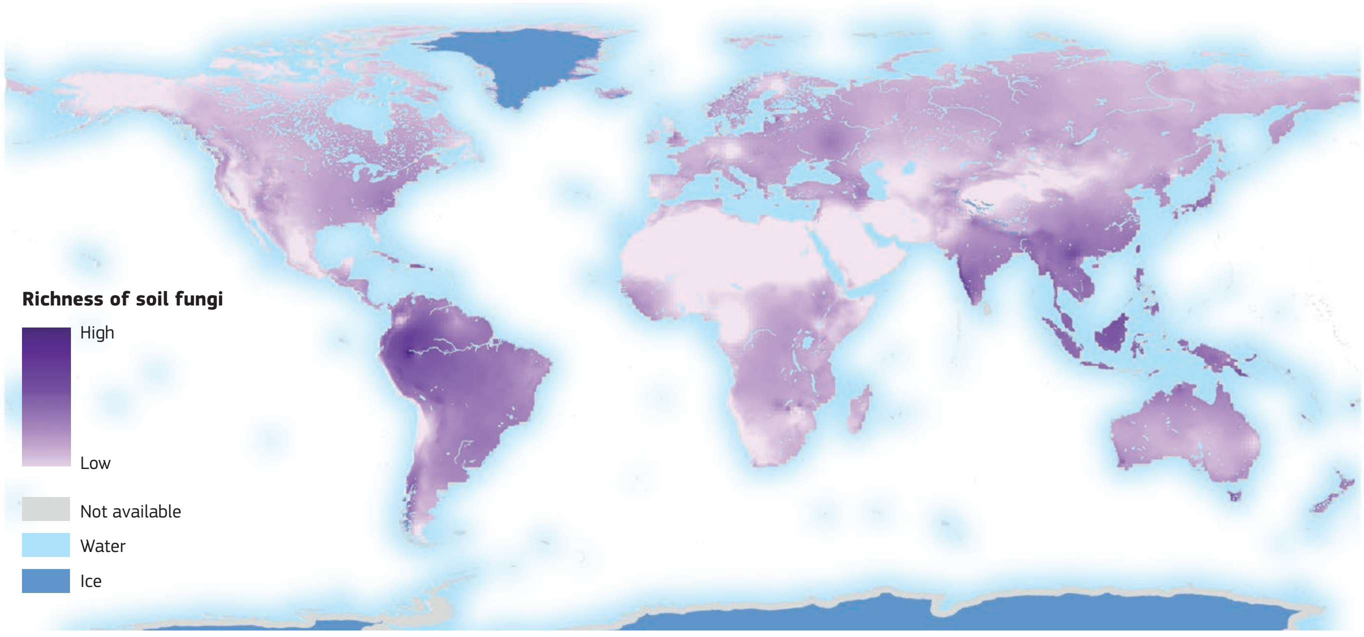
Nematode distribution

Nematodes (see pages 46-47) have successfully established themselves in all ecosystem types, including soil, marine and freshwaters, as well as in harsh environments such as the hottest and coldest deserts on Earth. Soil nematodes are not evenly distributed across the landscape but vary in abundance, species numbers, size and feeding habits. Among the most abundant multicellular animals on Earth (estimated at more than 10^{19} individuals globally and up to millions of individuals per square metre of soil), the diversity and abundance of nematode species can vary at local and global spatial scales. [86]

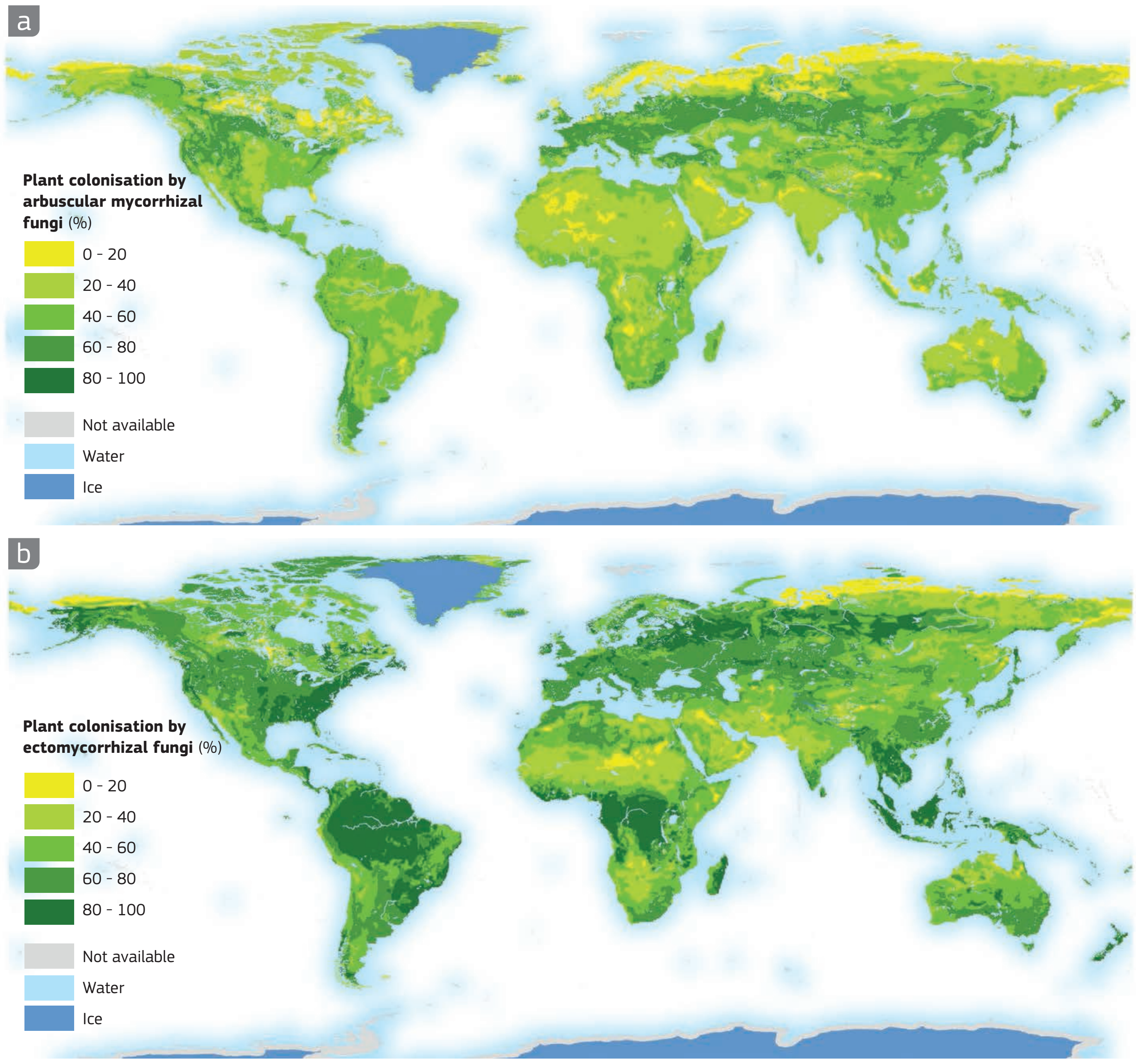
A plant parasitic nematode feeding on a plant root. The presence of host plants is a key factor influencing the distribution of this group of nematodes. (OB)

On a global scale, nematode diversity does not seem to follow patterns of aboveground diversity, which increases in the tropics and declines with increasing latitudes toward the geographic poles. Instead, nematode diversity appears to be high across most latitudes, decreasing only in the polar regions. Even at small scales (millimetres to centimetres), nematode species diversity can be high. For example, a single soil core (approx. 100 cubic centimetres) from a Cameroon forest contained 89 nematode species, while molecular tools are discovering increasingly high numbers of undescribed species.

Globally, nematode species distributions show distinct biogeographies, with many species endemic to particular regions or ecosystems. Although soil nematodes readily disperse in water (e.g. irrigation water and floods), by air and phoretically, global and continental patterns of nematode diversity are largely determined by climate, soil chemistry and plant community structure. Plant parasitic nematodes (PPNs) are codistributed globally with their hosts. The vast majority of PPNs have fairly narrow host ranges, while the most agriculturally damaging species tend to be more virulent and have broader host ranges.



Map of global taxonomic richness of soil fungi derived from the sequencing of DNA extracted from soil. Taxonomic richness is measured in terms of Operational Taxonomic Units (OTUs). OTUs are groups of DNA sequences with a level of similarity such that they are assumed to come from the same fungal species. To generate this map, the taxonomic richness of soil fungi was calculated based on mean annual precipitation, which has been assessed as being the most important driver of soil fungal diversity. Dark purple indicates rich sites, whereas light purple indicates sites with less estimated diversity (derived from Tedersoo *et al.*, Science, 2014). (JRC) [87]



Maps showing distinct levels (0 - 100 %) of plant root colonisation by (**a**) arbuscular and (**b**) ecto-mycorrhizal fungi, as conditioned by soil and climate. The map data result from the analysis of relationships between site-level data on intensity of root colonisation by arbuscular mycorrhizal and ectomycorrhizal fungi, and site soil and climate conditions data. The data do not show the actual (observed) levels of root colonisation by mycorrhizal fungi, but the colonisation levels predicted by environmental characteristics (which in total explained around 50 - 60 % of the observed distribution colonisation intensity – derived from Soudzilovskaia *et al.*, Global Ecology and Biogeography, 2015). (JRC) [88]

Insect-associated nematodes are also codistributed with their hosts and are found on every continent, except Antarctica. Similar to the PPNs, entomophilic nematodes follow patterns of virulence, host-specificity and biogeography.

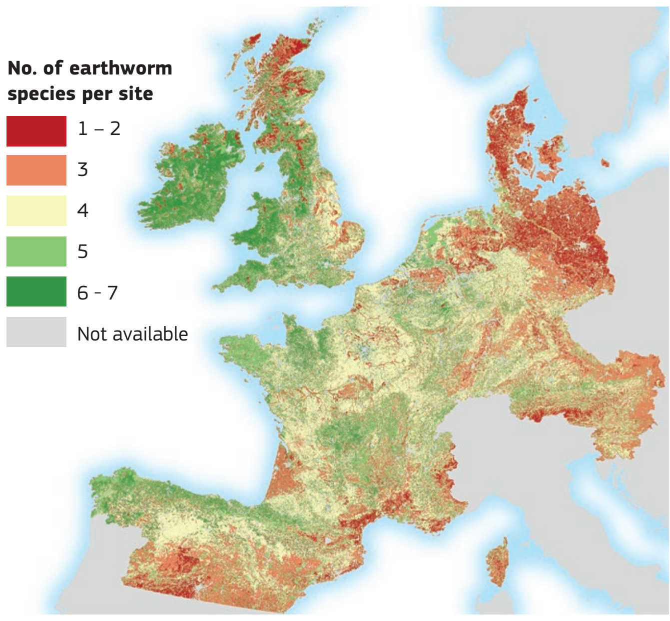
Nematodes that are not parasites or pathogens are the most diverse, and typically the most abundant, forms. This group includes the microbivorous nematodes. These nematodes have the broadest geographic distribution (globally) and occupy the most environmentally extreme habitats. Other members of this group include those that feed on cyanobacteria, algae and protists. These nematodes do not appear to be dispersal-limited, and can be found wherever there is suitable habitat. At small spatial scales, nematode distributions are often highly heterogeneous.

Even at larger spatial scales (hectares), nematode feeding groups, such as fungal-feeding nematodes, may not cluster together in a single hot-spot location. Instead they distribute as a function of soil moisture, plant species or other soil characteristics. Information on the factors determining the distribution of nematodes is critical for economic reasons. For example, plant parasitic nematodes can cause tremendous crop damage, entomopathogenic nematodes can provide effective control of insect pests, and nonparasitic species play crucial roles in nutrient cycling support for higher trophic levels. How climate change will alter soils, plant communities and nematode biogeography forms the basis of critical research currently underway. Additional studies aim to understand the linkage between host plant and nematode parasites, and the varied and complex contributions of nematodes to soil system structure and functioning.

Earthworm distribution

Earthworms (see page 58) represent one of the main taxonomic groups of soil biota. Earthworms are present in almost all terrestrial ecosystems at varying biomass, density or species richness levels. The distribution of earthworms and the structure of their communities is linked to evolutionary and ecological factors operating at different scales, from global to local. The present global distribution of earthworms is determined by different biotic and abiotic processes. [89]

During the past five centuries, human activities deeply impacted this global distribution by displacing earthworm species generally by accident. For example, many lumbricid species were introduced in New Zealand where communities were dominated by members of the families Acanthodrilidae and Megascolecidae; and a species (*Pontoscolex corethurus*) originating in South America is now found in all tropical lands. After introduction, these exotic species compete with native species, which deeply modify earthworm community structure and soil functioning. Earthworms originate from aquatic organisms, so they still need a minimum amount of liquid water to live. Consequently, they are absent from the coldest (poles and high mountains) and driest regions (deserts) on Earth. Earthworms can, therefore, be found in almost all climates and all latitudes. Only boreal forests lack earthworms, for historical reasons (glaciations). Actually about 7 000 earthworm species have been described for an estimated number of 30 000 existing species on Earth. Many species remain to be discovered and described, especially from tropical regions where earthworm species seem to be highly diversified.

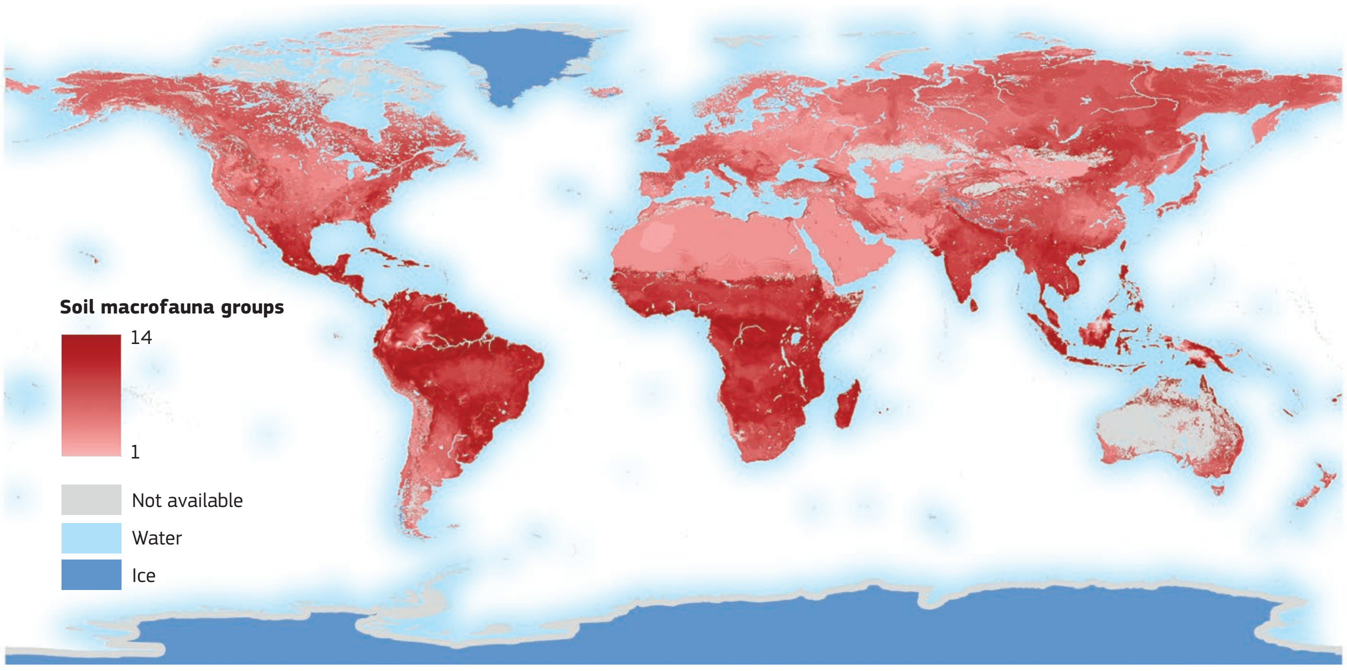


Predicted species richness of earthworms in some European countries. Existing datasets of earthworm communities in Europe were collected and modelled to depict a first earthworm biodiversity map in Europe. Earthworm community data were related to soil characteristics, land use, vegetation and climate factors. The analysis shows that land use and geological history are the most relevant factors determining the demography and diversity of earthworms across Europe. Grasslands and a temperate (humid) climate seem to favour the richness of earthworm communities, while dry conditions and arable land appear to be less favourable, as can be seen, for instance, in France. Unfortunately, this kind of analysis is not possible at a global scale because of the incompleteness of the available data. However, the map demonstrates the importance and efficiency of large databases for the detection of regional spatial patterns that could subsequently be applied at global scale (derived from Rutgers *et al.*, Applied Soil Ecology, 2016). [90]

Earthworm cocoons in French Guiana. Moisture is a key driver of earthworm distribution since the worms will cease reproduction when there is too little moisture. (TD)

At a more local scale, earthworms have to adapt to the environment including both abiotic (e.g. climate, soil type, soil texture and pH) and biotic factors (e.g. food resource, litter quality and predators). They have also to face recent anthropogenic changes (i.e. habitat alteration, invasive species and climate change – see Chapter V). Earthworms are relatively fragile organisms, and disturbances generally result in a loss of species. In the Western Ghats in South India, in a small area (10 km^2), 10 species were collected from altitude natural grassland, 7 - 8 species from forests, and 4 species from degraded pastures resulting from deforestation. It is interesting to note that all over the world there seems to be a systematic limitation of community richness to 10 - 12 species in undisturbed ecosystems.

Competition seems not to be an important factor in structuring earthworm communities, because different niches are available and earthworm species have developed specific functional traits (feeding on rich soil, poor soil, humified organic matter, freshly decomposed litter; living in litter, at the soil surface or deep in the ground). Nevertheless, competition pressure occurs in productive ecosystems where resources are scarce. At the ecosystem scale, earthworm density varies from zero to some hundreds of worms per square metre (about 1 000 individuals per m^2 in some temperate sites), and biomass ranges from zero to a few tonnes per hectare (more than four tonnes/ha in Normandy pastures in France). At a microscale, earthworm assemblages are usually spatially structured in patches ranging from a few tens of centimetres to a few tens of metres. This may be related to soil properties, vegetation and biotic factors (e.g. competition).



Number of co-occurring soil macrofauna groups in a 25 × 25 cm soil sample. The 14 groups included are: earthworms, ants, termites, spiders, millipedes, centipedes, isopods, fly larvae, cockroaches and mantids, moth and butterfly larvae, grasshoppers and crickets, gastropods, beetles and other macrofauna (see Chapter II). The distribution was assessed using a species distribution model for each group in relation to bioclimatic variables, land use cover and altitude (developed by Mathieu, 2015). (JRC)

Termite distribution

Termites (see page 55) are generally tropical animals, but their spatial distribution reaches into colder and drier environments. Indeed, they occur in five major biomes: tropical rain forests, tropical savannah woodlands, semi-deserts, temperate woodland and temperate rain forests (see pages 78, 82). Termite distribution is not uniform; in temperate regions their presence is nearly negligible, while in tropical areas they can be the dominant insects in the soil. [91]

Queen of *Nasutitermes coxipoensis* surrounded by workers and soldiers. This species has a wide distribution, particularly in north-western Brazil. (RC)

Nevertheless, patterns of termite distribution are very asymmetrical within the tropical regions. For example, species of the genus *Macrotermes* can be easily found in savannahs and forests of Africa and Asia, but not in South America and Australia. Local species richness is influenced by environmental factors. Rainfall, vegetation type, temperature and altitude have all been shown to influence termite diversity.

In general, the highest species richness is found in tropical forests (62 genera retrieved in the African Congolese rain forest). Temperate woodlands and rain forests have the lowest richness, with an average of three genera or fewer. The semi-deserts have more genera than the temperate ecosystems. The distribution of termites has also been studied in relation to their feeding preferences. Soil- and humus-feeding termites have their highest generic richness in the African, Neotropical (South and Central America) and Asian tropical rain forests. By contrast, wood-feeding termites are more evenly distributed across all biomes.

Ant distribution

- The Global Ant Biodiversity Informatics (GABI) project is an ongoing effort to consolidate and manage a comprehensive global database of ant species distributional records, including literature records, museum databases, and online specimen databases. [92]
- In 2015, GABI presented a website (antmaps.org) to visualise the known distribution of ant species or higher taxa across the world.
- Researchers at the University of Hong Kong in China and Japan's Okinawa Institute of Science and Technology developed the tool.
- The website features a series of interactive maps showing where each of the world's ca. 15 000 known ant species can be found.
- For example, the maps show that Greenland and Iceland have no native ant species, whereas Queensland (Australia) has the highest diversity, with 1 458 species.
- The database used to develop the maps, includes records from over 8 400 scientific publications, most major digitized museum collections, and online databases such as AntWeb. In total, the database contains over 1.6 million records.

Iridomyrmex splendens is one of the 1 458 ant species that can be found in Queensland (Australia), the region with the highest ant diversity in the world. (SSH)

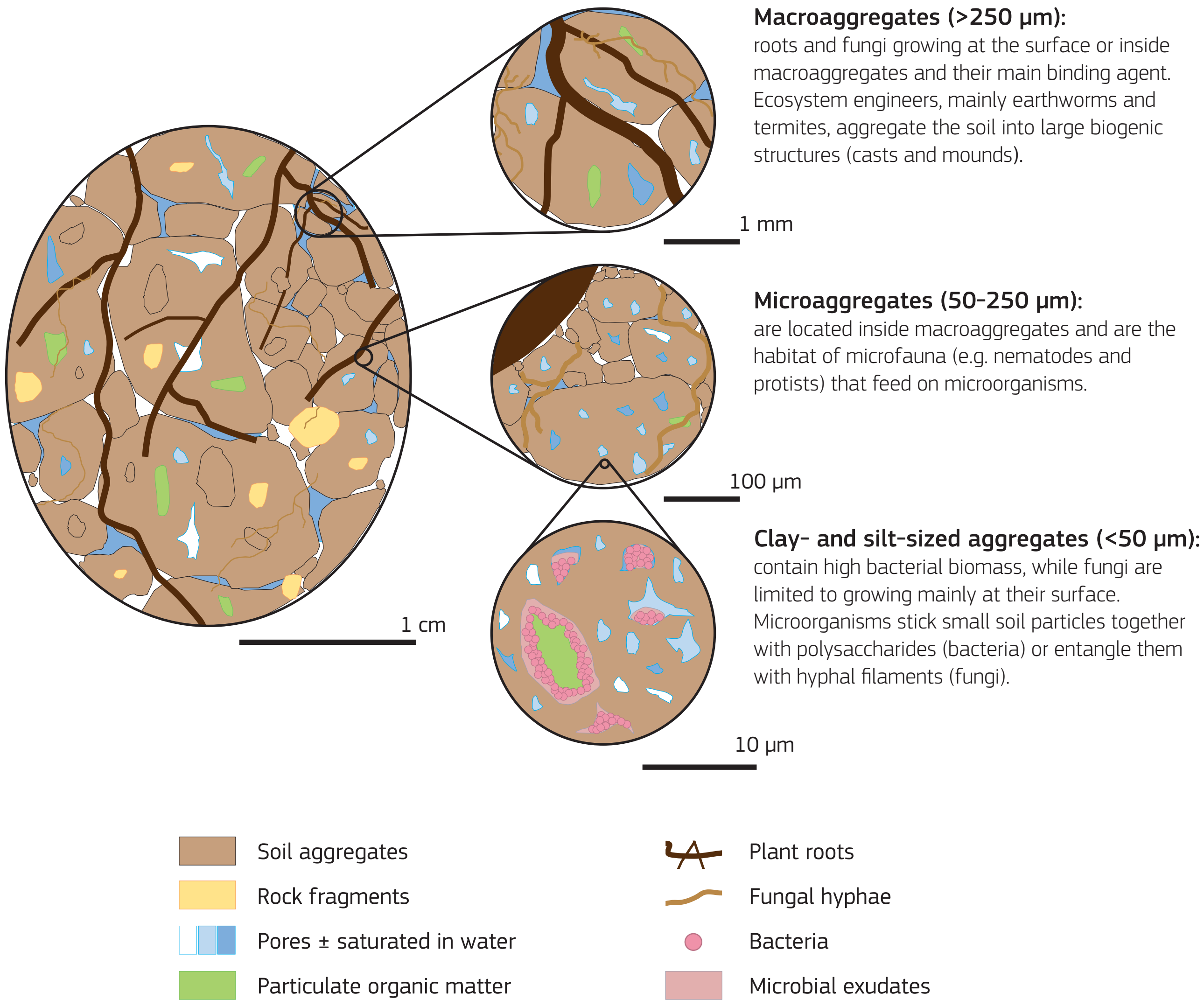
Distribution patterns – Soil biodiversity at aggregate scale

Soil aggregates

Soil is an incredibly complex and diverse organisation of pores and particles, which influence the organisms that live within. These particles, known as 'soil aggregates', consist of mineral and organic materials bound together, and are generally defined by their size and their stability in water. These aggregates are typically classified into three main size fractions: macroaggregates (> 250 µm), microaggregates (50 - 250 µm) and clay- and silt-sized aggregates (< 50 µm). Different soil organisms live in the network of pores between and within aggregates. [93]

The vast variation in the size of aggregates, as well as their physical-chemical properties, results in a huge diversity of microhabitats for organisms living within the soil. For example, small pores found in clay- and silt-sized aggregates will protect microorganisms (e.g. bacteria – see pages 33-35) against predation from larger organisms, which are restricted to larger pores in meso- and macroaggregates or between aggregates, and also restrict the flow of water and air and the input of new nutrients. Therefore, clay- and silt-sized aggregates are more stable habitats, with reduced competition and predation, and less variation in water influx (due to the capacity of small pores to better hold water), and are less sensitive to mechanical breakdown and influx of environmental pollutants.

Microaggregates are intermediate habitats, mainly populated by microfauna (e.g. nematodes – see pages 46-47). Macroaggregates are considered to be less stable habitats due to greater fluctuations in water and gas flow, increased competition and predation, and their sensitivity to mechanical breakdown (e.g. due to soil tillage, rain and drought cycles – see pages 15, 122-123). Macroaggregates are mostly populated by ecosystem engineers (see box on page 95), such as earthworms and termites (see pages 55, 58).



Overview of soil aggregates and the distribution of organisms at the aggregate scale. Due to the small sizes, the main inhabitants at aggregate scale are microorganisms, namely bacteria and fungi. (ABL)

The different sizes of soil aggregates. Soil structure is determined by how individual soil granules bind together and aggregate and, therefore, by the arrangement of soil pores between them. (ABL)

Microorganisms and soil aggregates

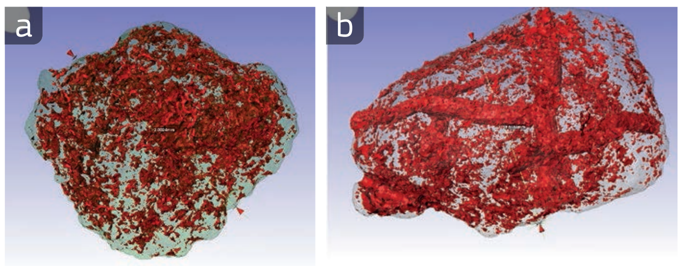
The abundance of microorganisms varies with the size of soil aggregates, and is directly related to the specific environmental conditions of each size. Bacterial biomass is often higher in clay- and silt-sized aggregates, especially in fine soil fractions (< 20 µm), where it can reach levels that are 30 - 80 % higher than in macroaggregates, due to more stable environmental conditions. Aerobic (life in the presence of oxygen) bacteria dominate macroaggregates, as oxygen concentration is higher; clay- and silt-sized aggregates generally contain a mix of aerobic and strict anaerobic (oxygen not needed to live) bacteria. By contrast, fungi (see pages 38-41) are mainly found in macroaggregates where their biomass and hyphae length can be up to 80 % higher than in microaggregates. The small size of pores in microaggregates prevents fungi from growing inside them, limiting the fungal presence to their surface.

The size of soil aggregates plays a role not only in microbial abundance, but also in diversity. For instance, bacterial diversity is often higher in microaggregates than macroaggregates. There is no general pattern in the distribution of bacterial phyla associated with a specific size of soil aggregates across different soils; however, Alphaproteobacteria (see page 34) are more often found to be associated with macroaggregates, Actinobacteria (see page 35) with microaggregates and species of the genus *Acidobacterium* with the fine soil fraction. The variation in bacterial diversity between sizes of soil aggregates has been suggested to be driven by the quality of soil organic matter in each size, rather than by its quantity. However, knowledge and understanding of the microbial diversity at the scale of soil aggregates remains limited and requires further research.

Functions at aggregate scale

In addition to microbial diversity and distribution, variation in soil aggregates also affects the functions carried out by microorganisms. For example, the composition of free-living bacteria that fix atmospheric nitrogen into soils (so-called diazotrophs – see page 99), differs with the size of soil aggregates. Macroaggregates have a greater diversity and activity of diazotrophs, yet microaggregates can carry between 30 % and 90 % of the diazotrophic population. These different diazotroph communities exploit specific anaerobic niches within the different sizes of aggregates, creating the conditions required for the fixation of nitrogen.

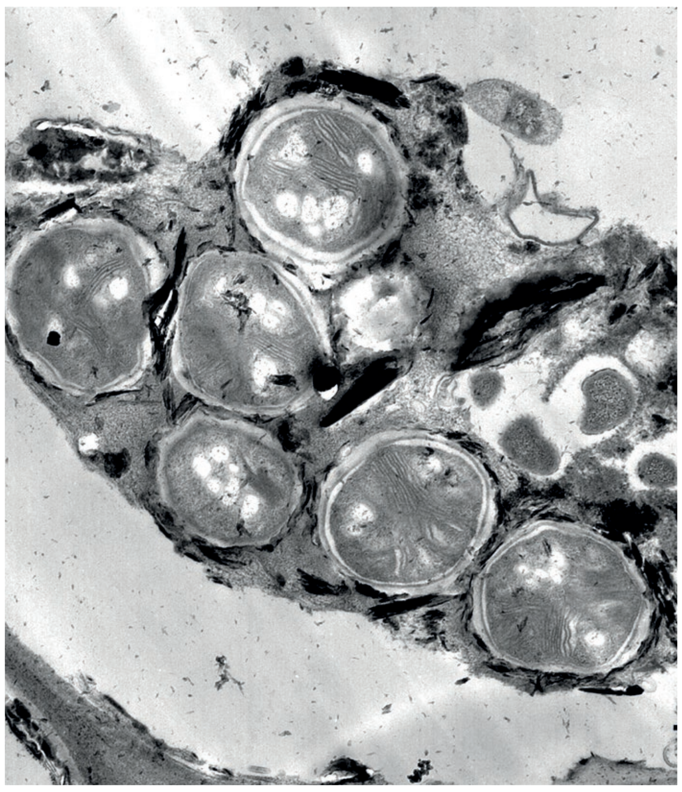
Similarly, denitrifiers, which reduce nitrate by releasing it back into the atmosphere (in a process called denitrification), are not present and active in all sizes of soil aggregates, but occur mainly in microaggregates, where nearly 90 % of the potential denitrification activity can occur. Furthermore, microbial diversity and functions can differ in relation to the location of microorganisms in the exterior or interior parts of aggregates. The process of nitrification (i.e. conversion of ammonium into nitrate) can be 50 % higher on the exterior of the aggregates (first mm) than in the interior, due to the aerobic conditions which are required for this process. Conversely, the interior of soil aggregates can provide anaerobic conditions favourable for processes that require low levels of oxygen, such as nitrogen fixation, denitrification or methane production. The interior of aggregates can also protect bacteria against pollutants, such as heavy metals, whereas the bacteria on the exterior of aggregates generally show more resistance to pollutants.



X-ray microtomography images of soil aggregates (~ 2 mm in size), from (**a**) cropland and (**b**) grassland. The pores, in red, where microorganisms live and develop, are small and fragmented in cropland aggregates. They are larger in grasslands due to the higher presence of roots. (MME)

Earthworms and aggregates

In most soils, earthworms (see page 58) play a key role in the formation of aggregates. These biogenic aggregates (earthworm-accumulated casts) may represent more than 50 % of the soil volume, and earthworms are considered as fundamental agents of aggregation in soil. Different organisms living within the soil are influenced by soil aggregates, and *vice versa*. This close interaction between soil biodiversity and soil aggregates is dynamic and can change over a short period of time. Therefore, soil management (e.g. conventional field tillage) can greatly affect the soil aggregates and organisms, meaning that better soil management is required to sustain the organisms and their microhabitats, in order to deliver valuable ecosystem services (see Chapter IV).



Transmission electron microscopy image shows bacteria living within a soil aggregate (cast) created by earthworms. (FW)

Distribution patterns – Soil biodiversity at the extremes

The Critical Zone

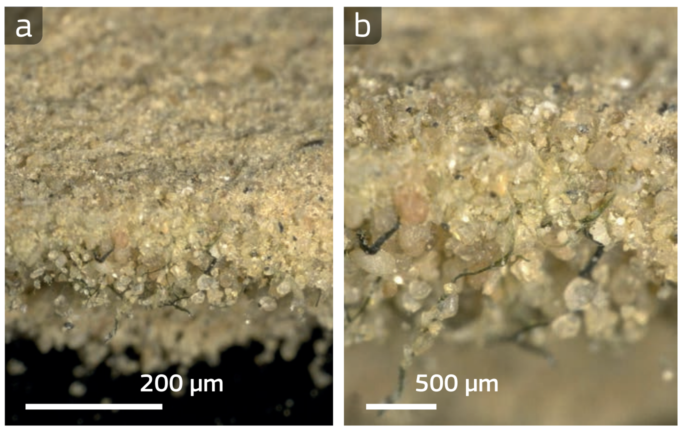
The concept of 'critical zone' is becoming central to ecological thinking, and is defined as the area above and below the soil surface that is critical to life on Earth. Generally, the belowground portion of the critical zone is defined by plant roots; therefore, the critical zone in forests is thought of as being several metres deep. However, in drylands, the situation may be very different. Most precipitation events are less than 5 mm, meaning that most microbial activity, nutrient cycling, and other processes crucial to ecosystem functioning, also occur at soil surfaces which are dominated by biocrusts. Therefore, in dryland regions, the biocrusts may well define the critical zone. [94]

Biodiversity at the soil surface

Soil organisms are distributed not only horizontally across different ecosystems on Earth, but also vertically, from the surface to the deeper soil layers, passing through the aggregates (see page 72). The most evident and visible example of soil biodiversity on the superficial layer of soil are biological crusts. Biological soil crusts, or biocrusts, are found in most ecosystems where plant cover is limited. This includes hot, cool, and polar deserts, as well as steppe and sub-humid regions (see pages 86-87). [95]

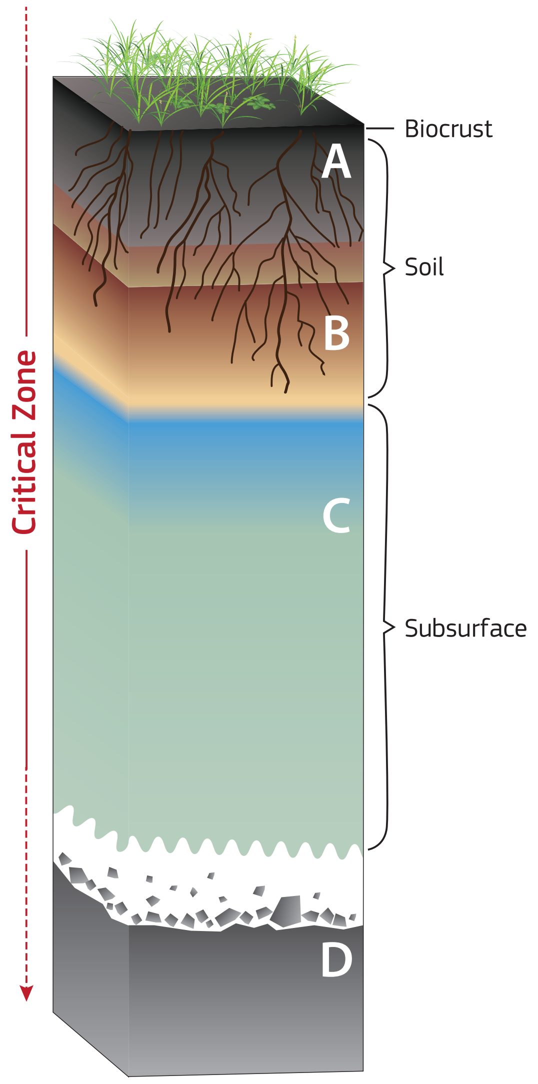
Biocrusts are communities of microorganisms (bacteria, cyanobacteria, fungi and green algae – see pages 33-35, 38-41) together with macroscopic lichens (see page 42) and mosses that cover most of the soil surfaces between the plants. The biodiversity found in biocrusts often far exceeds that of the plant community in which they are embedded, as they contain hundreds to thousands of species, whereas most plant communities contain fewer than 100 species.

Biocrusts play many essential roles in the ecosystems in which they occur and, as the biomass of the biocrust organisms increases, their influence on ecosystem processes increases as well. All biocrust organisms are integral to the formation and stabilisation of soils, and are believed to have been playing this role since they first appeared on land about one thousand million years ago. They accelerate soil weathering (see page 20), altering soil pH by secreting acids and ions (Ca^{2+} and OH^{-}). They also delay evaporation of soil moisture, thereby increasing rock and soil weathering by increasing the length of time these materials are wet.



Panoramic view of (**a-b**) two different magnifications of a cyanobacterial biological soil crust from the Negev Desert, Israel. The green filamentous cyanobacterial species *Microcoleus* is hiding from the sunlight under a thin layer of atmospheric dust, so that it is hardly visible on the crusts' surface. (VF)

Biocrusts are vital in soil stabilisation, especially in regions with low cover of other soil stabilisers, such as plants. Stabilisation is mostly a result of cyanobacterial and fungal filaments moving through the soil, as well as across its surface, leaving behind a trail of the sticky, mucilaginous sheath material that binds soil particles together. Lichens and mosses also protect the soil surface from exposure to wind or water, reducing the detachment of soil particles. Combined, biocrust organisms greatly reduce or even eliminate soil erosion in dryland regions. Biocrusts play other ecosystem roles as well. Cyanobacteria, green algae, lichens and mosses are all photosynthetic and, thus, contribute crucial carbon (C) to dryland soils. Carbon content (see page 104) is often very low in these soils and can limit microbial activity, thus slowing nutrient transformation and decomposition. The contribution of C by biocrusts can be substantial, often equivalent to the soil being covered by a vascular plant leaf. Nitrogen (see page 105) is also contributed to soils by free-living and lichenised cyanobacteria, and it is often the dominant source of this often-limiting nutrient. The nitrogen contribution by biocrusts has been estimated to be of global significance.



The Earth's critical zone is defined as the heterogeneous, near surface environment in which complex interactions involving rock, soil, water, air and living organisms regulate the natural habitat and determine the availability of life-sustaining resources. The critical zone, where soil biodiversity is present, ranges from the outer extent of vegetation down through the lower limits of groundwater, including the soil biocrust (in drylands), soil, altered rock and the zone saturated by water. A = topsoil, B = subsoil, C = zone saturated by water and D = rock (derived from Akob and Küsel, Biogeosciences, 2011). [96]

Biodiversity in the subsurface

Most studies of the interactions between life aboveground and life belowground have concentrated primarily on connections between vegetation, soil and the uppermost layer of weathered rocks, rarely investigating more than a metre below the surface. Although the processes taking place in deeper zones may profoundly influence life at the surface, important questions remain about the links between the deep biosphere and surface environments, including the soil: how does land use or disturbance at the surface impact the subsurface? How are signals, if any, transported from the surface to the deep biosphere? How long does this take and how long does it last? [96]

Deep life, defined here as beginning below the rooting zone, often extends far below the pedosphere, down through the subsurface to caves and groundwater contained within shallow and deep aquifers. Of course, prokaryotic (see page 30) population densities decrease with depth from the soil surface to the subsurface (see above), but levels of 10^4 to 10^8 cells per gramme can still be found in unsaturated bedrock or 10^3 to 10^8 cells per ml groundwater in saturated bedrock. The lower boundary of the deep biosphere, marking the limits of the influence of life on the rock environment, is still not defined. Molecular methods (see pages 64-65) have provided evidence that the biosphere can reach deep into the bedrock.

Assuming an upper temperature limit of 130 °C for bacteria, life could exist down to a depth of 5.2 km in continental crusts. Although the constraints of temperature, energy, oxygen and space should preclude life of multicellular organisms at these depths, nematodes feeding on subsurface bacteria have been detected in 3.6 km-deep fracture water in the deep mines of South Africa. Often flagellates, ciliates and amoeba are present, suggesting that protists (see pages 36-37) can make an important contribution to the control of microbial populations by grazing bacteria on rock surfaces. But still less is known about the role and distribution of deep biodiversity, in particular, what controls its spatial distribution, its role in shaping water and nutrient cycles (e.g. carbon and nitrogen), and the consequences for ecosystem services (see Chapter IV).

Studies of the first few metres of soil demonstrate large differences in the microbial community structure between surface soil communities and those living deeper than one metre. Probing even deeper into the subsurface raises a number of basic questions: What biota live there? How do they interact with and reflect their environment? And how do they reflect surface properties? Microbial communities living in the subsurface appear to be composed of many bacteria and archaea (see page 32) belonging to classes and orders that had not been previously sampled or even recognised. Some might belong to mostly uncharted branches of the tree of life, the 'microbial dark matter' that represents a major unexplored portion of microbial diversity.

Devil's worm

- Since their discovery over two decades ago, single-cell organisms were considered the only inhabitants of the deepest layers of soil.
- In 2011, a new species of nematode was recovered from 0.9-3.6 kilometre-deep fractures in the deep gold mines of South Africa.
- *Halicephalobus mephisto* was the name given to the new species, with mephisto, which means 'he who loves not the light', alluding to the Devil and referring to the German demon Mephistopheles.
- For this reason it is also commonly known as Devil's worm.
- According to radiocarbon dating, these worms live in groundwater that is 3 000-12 000 years old.
- *Halicephalobus mephisto* is resistant to high temperatures and feeds on subterranean bacteria. [97]

Impacts on the soil subsurface

Although less is known about the subsurface, humans are beginning to exert an increasing impact on this zone, both directly through activities like heat and energy exchange, and use for waste disposal or gas storage, but also indirectly through the downward communication of changes in the atmosphere and aboveground biodiversity. Since land use is a main driver of aboveground biodiversity change, land use intensification has frequently been shown to negatively affect biodiversity. But how deep can the 'fingerprints' of vegetation or land use be traced? Does the subsurface biodiversity really care about land use intensifications, about a decline in aboveground biodiversity?

Plant diversity can significantly influence the density and diversity of soil organisms, which in turn are likely to govern essential ecosystem processes. Plant diversity effects can be even more important for the structure and functioning of soil food webs (see page 96) than changes in atmospheric CO_2 concentrations or nitrogen depositions. Therefore, a loss of biodiversity could have at least as great an impact as other anthropogenic drivers of environmental change. Some investigations of the Earth's critical zone have been established in the past decade to improve our fundamental understanding of the biogeochemical processes in the subsurface and how they are linked to surface properties. Linear core drillings and groundwater wells grant access to the hidden subsurface compartment of the 'Critical Zone' and provide an understanding of how the provision of ecosystem services are ultimately linked with biodiversity and processes within the subsurface.

Soil cores are sampled in order to study soil biodiversity in deeper layers of the critical zone. (KKU)

Distribution patterns – Soil biodiversity over time

Hours and days

Soil biodiversity is not static. Populations of soil organisms change constantly over time, with changes in the structure and diversity of soil communities occurring over timescales of days to seasons, and even decades to millennia. A common feature of microbial populations in soil is that their abundance can change very rapidly, even over hours or days. Such rapid changes are caused by several factors, including predator-prey relationships and pulses in resource supply. After periods of drought, for example, sudden increases in soil water availability following rainfall events cause spectacular boosts in microbial growth and associated pulses of nitrogen mineralisation and carbon dioxide release from soil. The release of carbon-rich exudates into soil from roots also causes rapid increases in microbial growth, and the time taken from photosynthesis (see box on page 35) to the transfer of photosynthetic carbon to roots, mycorrhizal fungi (see page 40) and free-living soil microorganisms can take just hours in grassland or days in forests. Also, much of this photosynthetic carbon is lost from soil by heterotrophic respiration within a matter of hours or days, which points to the great importance of root exudation for short-term microbial dynamics in soil. [98]

Pulses in root exudation can also be triggered by defoliation events, or when roots are attacked by root herbivores, which stimulates microbial activity and nitrogen mineralisation in the soil surrounding the root, increasing plant nutrient uptake and growth. The following zones have abundant living communities that may vary over short periods of time: detritusphere (interface between soil and litter), rhizosphere (interface between soil and plant roots), mycorrhizosphere (interface between mycorrhizal hyphae and soil), mycosphere (interface between fungal hyphae and soil) and drilosphere (interface between earthworm burrows and soil). For example, according to a general rule (the Arrhenius equation), microbial processes increase by a factor of two when temperature increases by about 10 °C. Therefore, soil microorganism in their natural environment will be less active during the night than during the day.

Besides this direct effect of temperature on soil microorganisms, other indirect effects may also influence the daily rhythms of microbial behaviour. For example, plants assimilate carbon during the day and release some carbohydrates into the soil by root exudation at night.

Prehistoric soil biodiversity

- Thanks to new DNA-based techniques (see pages 64-65), it is possible to study palaeobiodiversity (i.e. ancient biodiversity).
- Because of its properties, permafrost (see page 16) is able to preserve ancient DNA.
- Permafrost is a soil that remains at or below the freezing point of water (0 °C) for two or more years.
- The theoretical limit of ancient DNA survival under ideal conditions, such as in permafrost, is about 1 million years.
- In 2012, researchers collected permafrost samples dated 16 000 - 32 000 years old from two localities in Siberia in order to study ancient soil fungal communities. [99]
- About one-third of the fungi found are presumed to be plant associates (pathogens, saprotrophs and symbionts) typical of grass-rich habitats.
- Pathogens likely associated with ancient insects were also found.

Frozen soils preserve DNA that can be used to study ancient soil biodiversity communities. (JBR)

As temperature, moisture and plant cover change throughout the seasons, from (**a**) winter to (**b**) spring, from (**c**) summer to (**d**) autumn, the same goes for soil communities. (CK, KRE, TO, MBA)

Seasons and years

Soil communities also change in abundance and composition throughout seasons and years, caused by seasonal and inter-annual changes in precipitation and temperature, disturbance events linked to land use, and also the seasonality of plant growth. In some situations, seasonal shifts in soil communities are relatively distinct, for example in alpine soils where microbial communities display a complete turnover between winter and summer, with taxonomically and functionally distinct communities occurring at both times.

In other situations, however, communities can be very complex and apparently chaotic over time. In agricultural soils, for example, seasonal and inter-annual patterns in soil animal and microbial communities vary with land use and agronomic practices, including crop type and fertiliser regimes, as well as with soil type. Furthermore, effects of agronomic practices on soil organisms are likely to vary considerably at different times of the year, meaning that careful thought needs to go into how soil biodiversity is evaluated in field experiments to determine the effects of land management practices on the biology and functioning of soil. Moreover, seasonal and inter-annual patterns of soil biodiversity are complicated by the fact that many soil organisms can undergo long periods of inactivity when conditions are unfavourable, which allows them to tolerate periods of harsh soil conditions.

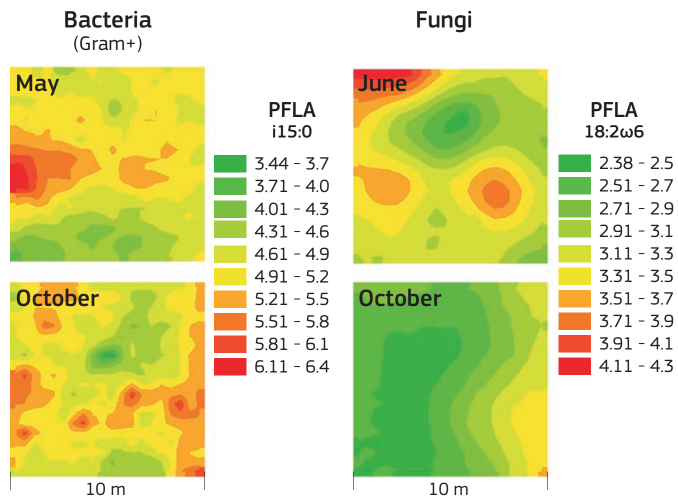
Roots and root exudates (fluids secreted through root pores) are among the most important drivers of microorganism growth (e.g. bacteria and fungi) in the short-term. They include acids, sugars, polysaccharides and enzymes. (MD)

The case of microorganisms in grasslands

Temporal variation in the abundance and function of soil microorganisms is especially high in topsoil (see page 10), because the most important drivers (i.e. food resources, temperature and moisture) vary considerably in topsoil throughout the seasons. In an experiment conducted in 2011, researchers tested whether the temporal distribution of a historically natural grassland in Germany changed throughout the growing season.

Microbial community spatial structure was found to be positively correlated with the local environment (i.e. physical and chemical soil properties – see Chapter I), in spring and autumn, while the density and diversity of plants had an additional effect in the summer period. Spatial relationships among plant and microbial communities were detected only in the early summer and autumn periods, when aboveground biomass increase was most rapid and its influence on soil microbial communities was greatest due to increased demand by plants for nutrients. The spatial distribution of Gram-positive (Gram+ – see box on page 34) bacteria and fungi (see pages 38-41) changed during the season. For example, the distribution of bacteria shifted from a cosmopolitan to a patchy distribution from May to October. This result may have been due to competition between bacteria and plants for nutrients. In particular, some of the most abundant Gram+ bacteria may suffer from nutrient limitation late in the season, and their growth could then be restricted to 'hot spots' in which nutrients are accessible.

The distribution of fungi was patchy early in the season, but in October it was almost uniform, providing evidence for the development of a wide distribution of fungal hyphae over time. This example clearly shows how soil communities change not only across space, but also across time. The assessment of temporal distribution must go hand in hand with the spatial analysis in order to better understand the dynamics of life in soil.



Temporal distribution of soil microorganisms in an unfertilised grassland in Germany. To describe soil microorganisms, the phospholipid fatty acid (PLFA) analysis was used (see pages 64-65). The PLFA i15:0 represents mainly Gram-positive (Gram+) bacteria and the PLFA 18:2ω6 represents fungi. Green colours characterise low abundance of different groups of microorganisms, whereas red colours indicate high abundance (derived from Regan *et al.*, Soil Biology and Biochemistry, 2014). [100]

Hundreds and thousands of years

Soil biodiversity also changes over hundreds or thousands of years, through processes of primary succession, which is the gradual and natural development of an ecosystem over a longer period of time. Studies have revealed a number of general patterns that occur in soil communities over these long timescales. Most data come from glacier forelands and lava fields, and sand dune systems, that undergo primary succession. These kinds of landscapes are unique observatories of soil formation because they contain soil chronosequences (sets of soils that differ only by age as they have developed on similar parent materials under the influence of similar abiotic and biotic factors). As succession proceeds from its initial stages toward the 'maximal biomass', or climax phase, soil microbial communities become increasingly abundant, active and diverse, and they also become increasingly fungal dominated (over bacteria) in nature. Mycorrhizal communities also change as succession proceeds: during early succession, ruderal plants are generally non-mycorrhizal, whereas in mid-succession, the dominant herbaceous plants tend to have a facultative requirement for arbuscular mycorrhizal fungi. Finally, in climax communities, the trees and shrubs, which dominate the vegetation, often have an obligate need for ectomycorrhizae (see page 40). [101]

Let's give some numbers

- Soil organisms that must cope with tight barriers of the soil are often small, move over short distances during their lifetime and colonise small patches that vary in spatial structure.
- This means that when land use changes, or habitats become fragmented, source-sink relationships occur between disturbed areas and 'refuge' areas containing passively dispersed organisms.
- To overcome the spatial constraints, the organisms often invest in temporal persistence rather than in dispersal to survive adverse environmental conditions, as for example dormancy of spores and seeds or inactive forms of soil invertebrates. Dormancy structures may allow organisms to survive over seasons and years.
- The majority of soil protists are present as resting cysts, and only a minor fraction are active cells.
- It is important to bear in mind that other members of the soil biota that do not go through morphologically recognisable resting stages (e.g. microarthropods) may also have periods without activity, as eggs or pre-moult phases.

Taxonomic group	Active range of individual	Passive dispersal	Dormancy stage
Basidiomycetes	> 100 metres (m)	100 - > 1 000 m	spores
Saprophytic fungi	0.003 - 0.005 m per day	100 - > 1 000 m	spores and conidia
AM fungi	0.005 m per day	0.01 - 1 m	spores
Bacteria	0.000001 m	not determined	inactive cells
Nematodes	0.01 m	> 10 000 m	dauer larvae
Protists	0.000001 m	< 100 000 m	cysts
Collembolans	0.1 - 100 m	> 1 000 m	eggs
Mites	0.01 - 0.1 m per day	> 1 000 m	eggs
Millipedes	1 - 20 m per day	not determined	adult hibernation and aestivation
Isopods	10 - 1 000 m	not determined	no

The spatial scale over which soil organisms actively move is generally over a millimetre to centimetre. Through their passive dispersal, propagules (structures of resistance – see box on page 34) of bacteria, fungi, protists and nematodes (see Chapter II) have been found thousands of metres from the source.

Similar changes in microbial community composition appear to occur during secondary succession. This process of succession occurs after land has suffered a major disturbance, such as fires or hurricanes, or following the abandonment of agricultural land. Such events commonly lead, over time, to a shift in the make-up of the microbial community toward fungal dominance over bacteria. These changes can take decades to occur and they are most likely related to a build-up in the amount and complexity of organic matter, and changes in the quality of resource inputs to soil resulting from vegetation change. They may also be related to changes in the physical-chemical nature of soils; for example, a decline in soil pH that commonly occurs during succession.

Soil animal communities also change during succession, but patterns appear to be less clear, at least when considering temporal changes in different trophic groups. For example, during secondary succession in abandoned agricultural land, soil invertebrates of different trophic groups appear to respond differently, and some faunal groups do not recover at all. Also, on glacier forelands, the first colonisers of recently exposed glacial debris can be predators, with herbivores and decomposers coming later.

Similarly, the first colonisers of newly exposed glacial moraine in the Arctic have been shown to be spiders (see page 61), whose densities are related to inputs of potential prey items, predominantly midges. In these harsh environments, large inputs of insects could be an important source of nutrients for the developing ecosystem, even before a cyanobacterial crust (see pages 35, 73) forms, Insects are often the first colonisers of newly exposed soils in extreme environments.

Many factors cause soil communities to change over successional timescales, but of most importance is the build-up in the amount of complexity of soil organic matter, which provides resources for the developing soil food web. This is largely driven by changes in vegetation as succession proceeds, which alter both the amount and quality of organic matter entering the soil, and also soil weathering processes (see page 20), which contribute to the formation of mature soils from early stages. In particular, processes of soil weathering determine the depth of soil, its pH and the availability of key nutrients, such as phosphorus. However, soil organisms themselves can also influence vegetation succession.

They do this via a process called plant-soil feedback, which is driven by root-associated symbionts and root pathogens (see box on page 39), which become more abundant and diverse as succession proceeds. As an example, arbuscular mycorrhizal fungi can increase plant species diversity in early successional communities, because they promote herbaceous species over dominant grasses, and increase transfers of nutrients among plants via hyphal networks, which results in nutrients being more evenly distributed among the plant community, thereby limiting the dominance of certain plant species. The build-up of root pathogens during succession can also exert a powerful influence on vegetation change. For example, the build-up of both root pathogens and root-feeding nematodes in the root zone of Marram grass (*Ammophila arenaria*) decreases in the abundance of this plant and causes its replacement by *Festuca rubra* (red fescue), that is not susceptible to these pathogens. Similarly, the build-up of insect root herbivores that feed selectively on early successional plant species enables late successional species to become established, thereby causing vegetation change.

(**a**) Glacial retreats and (**b**) lava fields are the perfect backdrop to set up a study of temporal effects on soil biodiversity, from primary stages to decline. The difficulty is due to time itself since very long periods are needed in order to see the long-term evolution of life in soil. (FKO, AS)

Millennia

Over timescales of millennia, ecosystems that have not been subject to catastrophic disturbance enter a 'decline phase' characterised by a reduction in tree biomass. This decline has been linked to long-term reductions in the availability of soil phosphorus, caused by thousands or millions of years of soil weathering, and the leaching and occlusion of phosphorus into non-biologically available forms. As a result, soil organic matter also becomes increasingly limited in phosphorus relative to other nutrients, such as nitrogen which is made available by biological nitrogen fixation (see page 105). A consequence of this is reduced substrate quality for decomposers, which contributes to reductions in the biomass of decomposer microbes and shifts in the composition of microbial communities toward increasing fungal dominance, which together act to curtail rates of litter decomposition and mineralisation of nutrients.

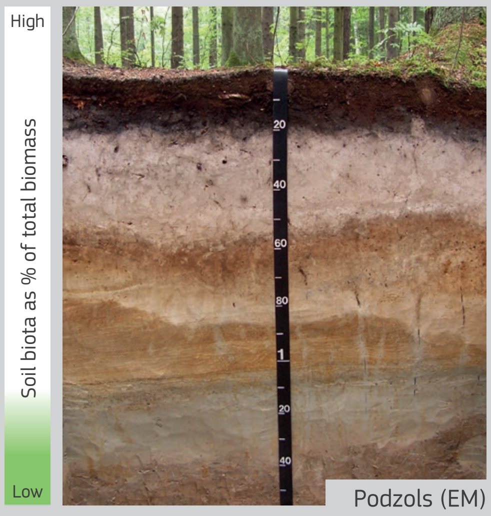
In other words, as ecosystems age and become increasingly limited in phosphorus, a negative feedback is set in motion whereby low foliar and litter nutrient status reduces decomposer activity, which further intensifies nutrient limitation, thereby leading to ecosystem decline. The entire soil food web (see page 96) is affected by these dynamics. However, effects on soil organisms other than microorganisms have been poorly studied. In New Zealand, it has been observed that the densities of microbial-feeding nematodes and enchytraeids (see pages 46-48) decrease when an ecosystem begins to decline, whereas the density of omnivorous nematodes initially increases, before also decreasing subsequently. The temporal distribution of microarthropods (e.g. mites, collembolans and myriapods – see pages 49-50, 57) has also been studied, showing contrasting patterns. For instance, in a boreal forest in north-eastern Canada, mites showed a significant decline in density and diversity during the decline phase, while no changes were found among collembolans. In conclusion, the very long-term dynamics of the whole soil biodiversity would need further investigation in order to better understand the role of all soil organisms in ecosystem development.

Soil biodiversity and ecoregions – Map of distribution across ecoregions

Temperate and Boreal Coniferous Forest

Temperate and boreal coniferous forest soils have fungal-dominated microbial communities; rich in decomposer and ectomycorrhizal fungi. Microarthopods and enchytraeid worms dominate the soil fauna, and ants are also abundant.

Podzols are distinctive soils characterised by the leaching of organic material, iron and aluminium from the A and E horizons, leaving behind a bleached layer. Leached material is redeposited as an organic/iron-rich cemented layer in the B horizon.

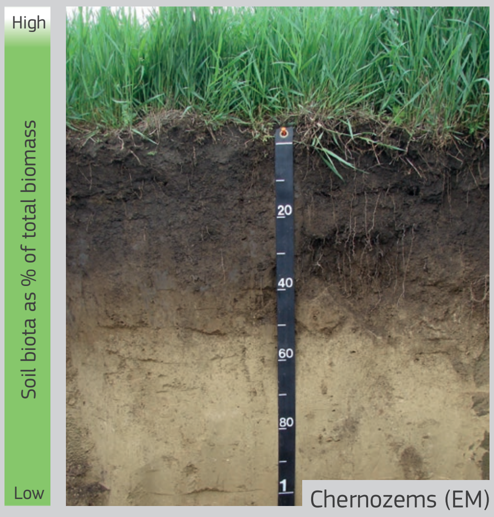


Podzols (EM)

Temperate Grassland

This ecoregion supports a high level of microbial and faunal diversity. Soils are characterised by a high abundance and diversity of arbuscular mycorrhizal fungi, earthworms, microarthropods and nematodes.

Chernozems are well-structured soils with a dark, organic-rich topsoil and secondary calcium carbonate in the subsoil. They support abundant natural grasses, typical of prairie or steppe landscapes. They grade to Phaeozems (wetter) or Kastanozems (drier).

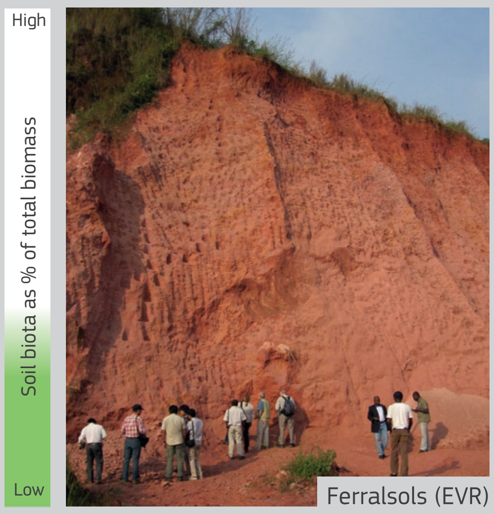


Chernozems (EM)

Tropical and Subtropical Forest

This ecoregion is characterised by highly diverse soils, with both arbuscular mycorrhizal and ectomycorrhizal fungi, and diverse and abundant communities of fauna, especially of termites, dung beetles, earthworms and nematodes.

Ferralsols are highly weathered coarse-textured soils with low pH, and are red or yellowish in colour due to high concentrations of iron and aluminium oxides. Organic matter levels are low. Horizons are absent due to intensive bioturbation, largely by termites.

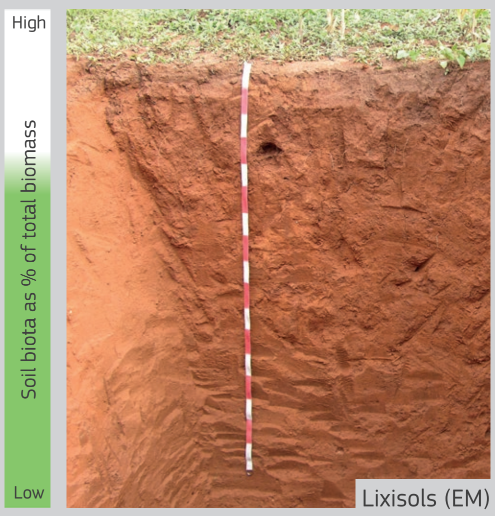


Ferralsols (EVR)

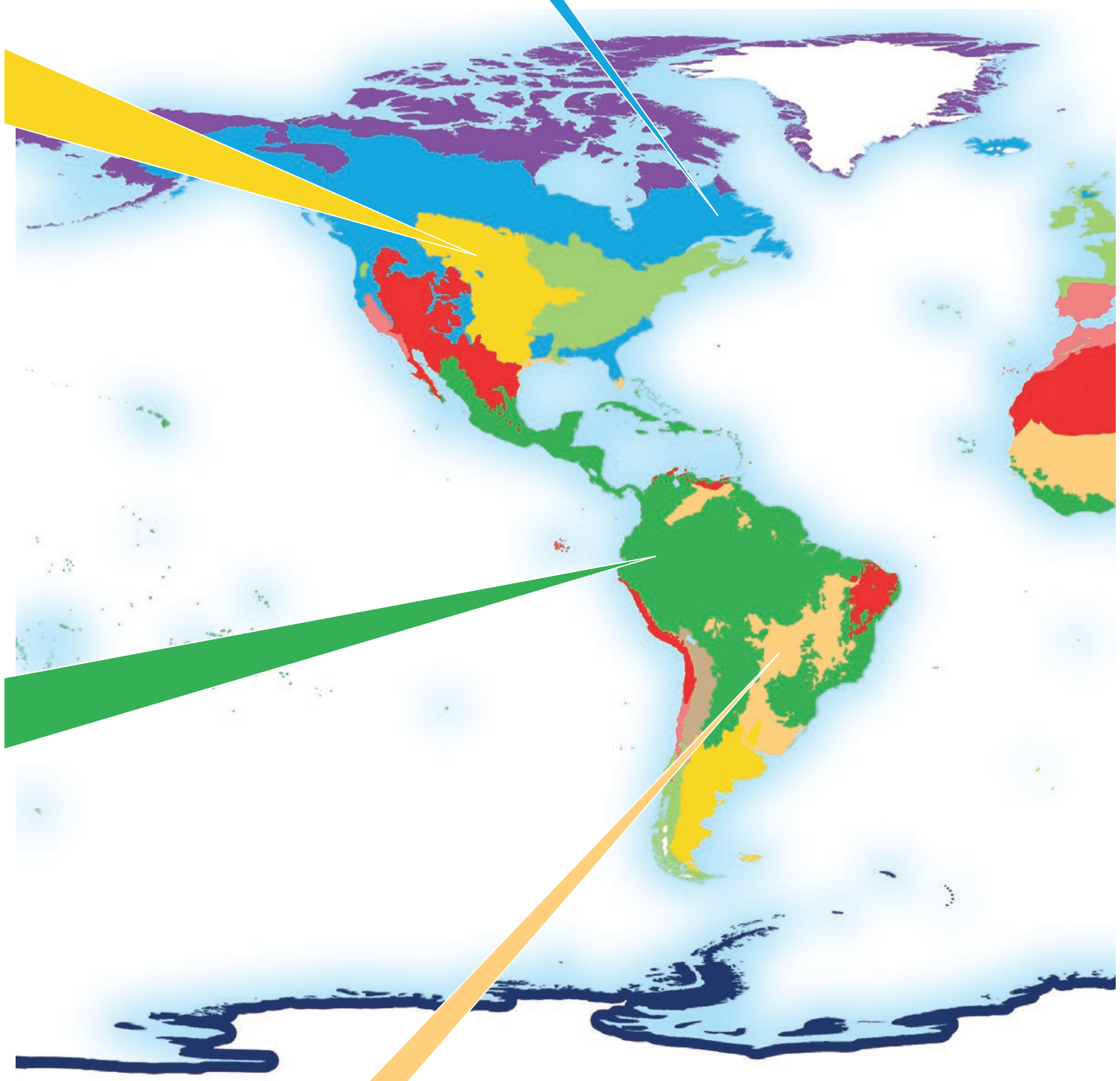
Tropical and Subtropical Grassland

Characteristic soil fauna in this ecoregion are termites and dung beetles, along with earthworms, microarthropods and nematodes. These soils contain a rich diversity of microorganisms, including arbuscular mycorrhizal fungi and nitrogen-fixing bacteria.

Lixisols are characteristic of drier conditions and exhibit subsurface accumulation of low activity clays with high base saturation as a result of limited leaching or inputs of airborne dust from adjacent deserts. Low in plant nutrients and prone to erosion.



Lixisols (EM)



Temperate Broadleaf and

Soil communities of this biome have high levels of microbial and faunal diversity, and contain abundant and diverse communities of fungi and macrofauna, especially earthworms.

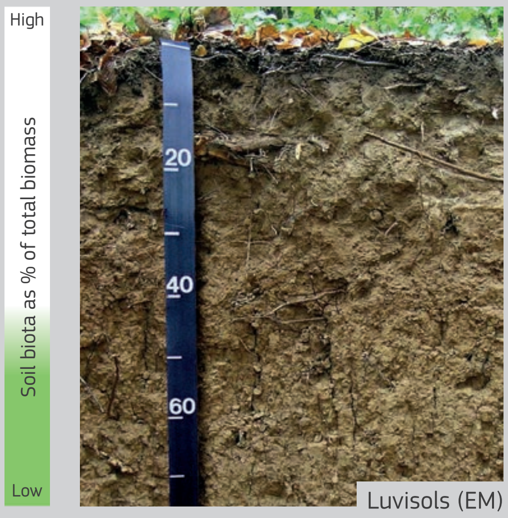
Luvisols are characterised by a clay-rich subsoil, often the result of movement of clay particles from the topsoil or the destruction of clay in the upper part of the soil. In general, neutral or slightly alkaline, they exhibit a well-defined, organic-rich A Horizon.

Antarctica

Soils with low diversity, especially in polar deserts. Besides microbes, only a few species, such as nematodes, tardigrades, rotifers and collembolans, are supported. Relatively species-rich communities of microarthropods can occur in some parts, while cyanobacterial communities are widely distributed.

The term ornithogenic means that the soil has been strongly influenced by the activity of birds (e.g. the continuous nesting of penguins) and shows an enrichment of phosphorus, calcium and potassium.

Mixed Forest

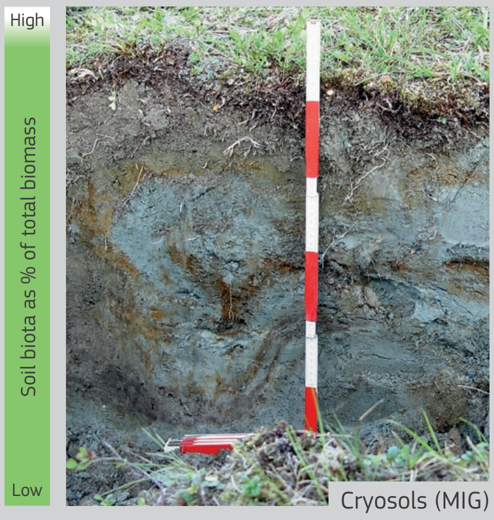


Luvisols (EM)

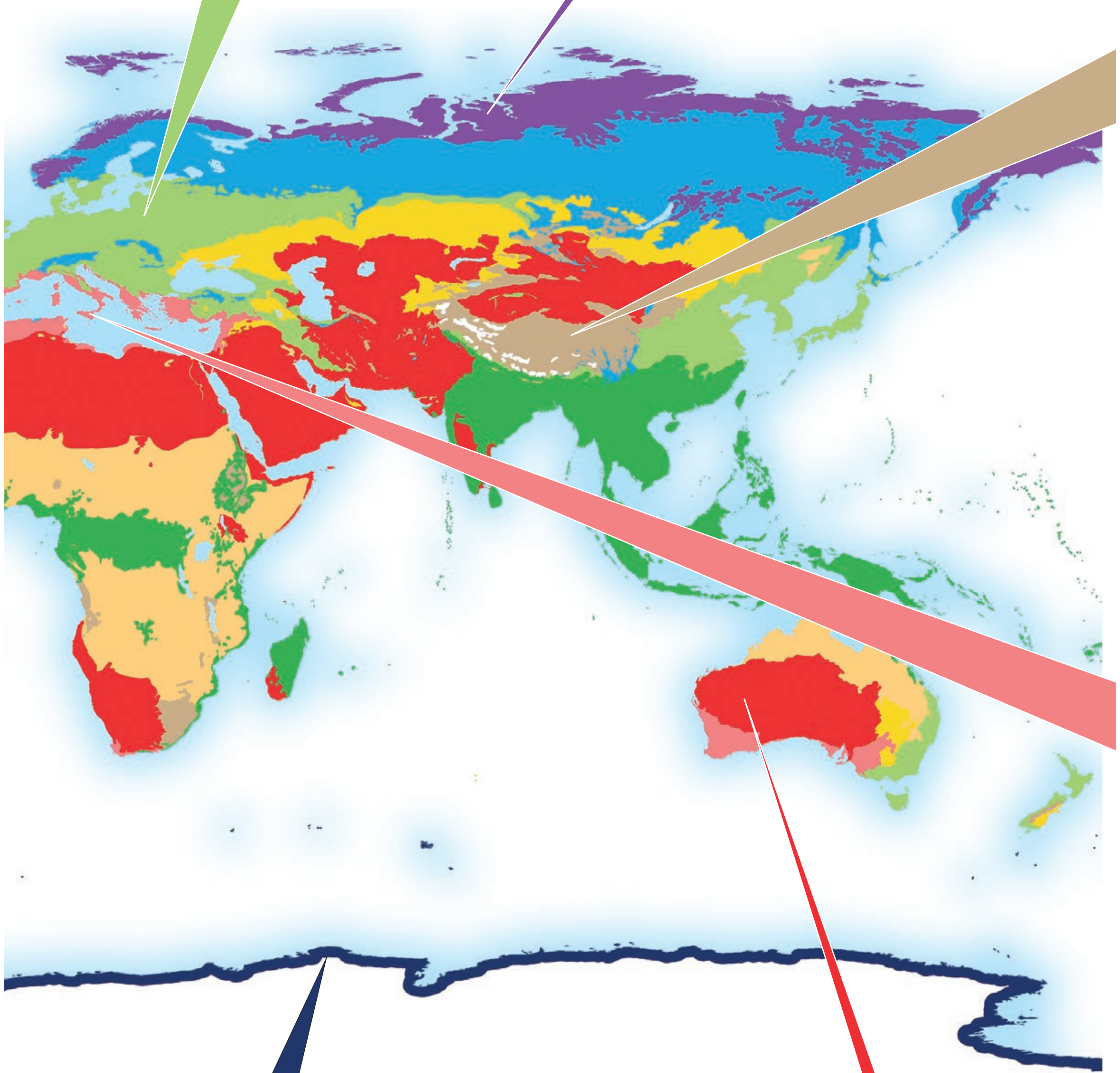
Tundra

Tundra soils support a relatively high diversity of fungal (both decomposer and mycorrhizal) and bacterial communities, together with a high diversity of nematodes and microarthropods, although, in terms of biomass, the dominant fauna are enchytraeid worms.

Cryosols are mineral or organic soils characterised by the presence of permafrost and waterlogging during periods of thawing. Cryosols can show distorted horizons, cracks or patterned surface features due to ice formation and melting.



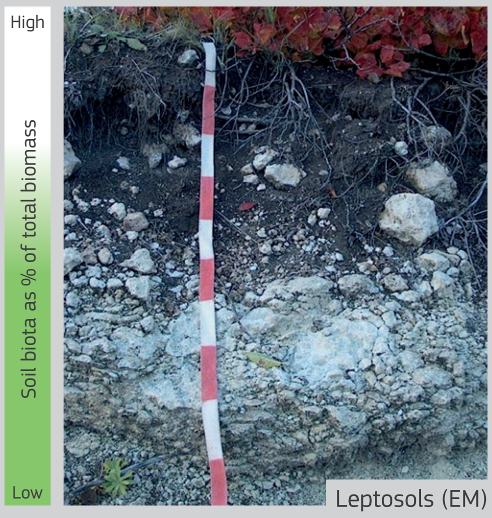
Cryosols (MIG)



Montane Grassland and Shrubland

Soils of this ecoregion are very variable, containing a high diversity of bacteria and fungi, and both arbuscular and ericoid mycorrhizal fungi. Nematodes, microarthropods and enchytraeid worms are species rich, but few earthworms are present.

Leptosols are shallow soils, often with large amounts of gravel, lacking well- defined horizons or strong signs of soil-forming processes. Generally found under natural vegetation, specific characteristics reflect local climatic and topographic conditions.

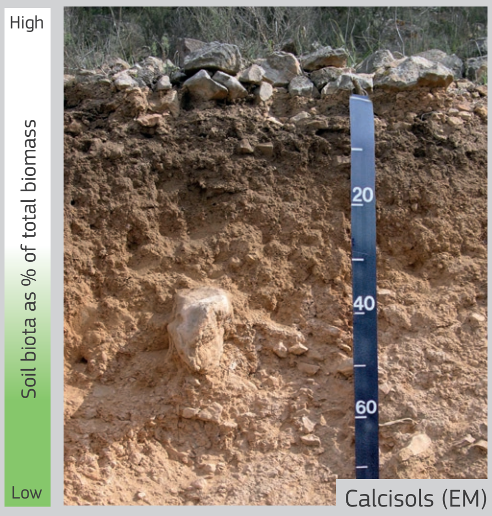


Leptosols (EM)

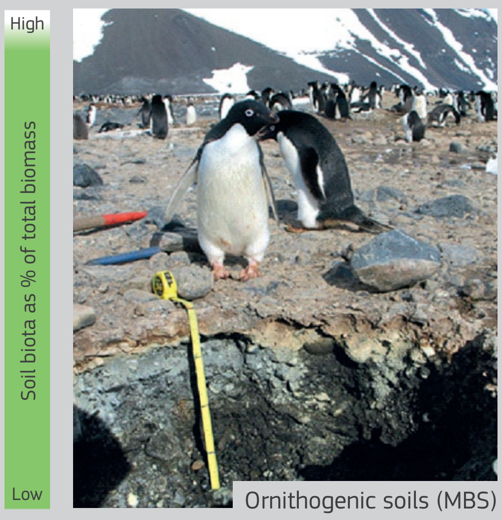
Mediterranean Forest, Woodland and Shrubland

Mediterranean soils are usually low in organic matter and, consequently, in soil biodiversity. The profusion of shrubs leads to an abundance of mycorrhizal fungi, and biocrusts are abundant. Soil fauna that withstand high temperatures (e.g. ants) are also widespread.

Calcisols are generally well-drained soils with high pH, fine- to medium-textured with a layer of migrated calcium carbonate in the subsoil which can be soft, powdery, hard or cemented. Their chief use is for animal grazing or grapevine, citrus fruit and olive cultivation.



Calcisols (EM)

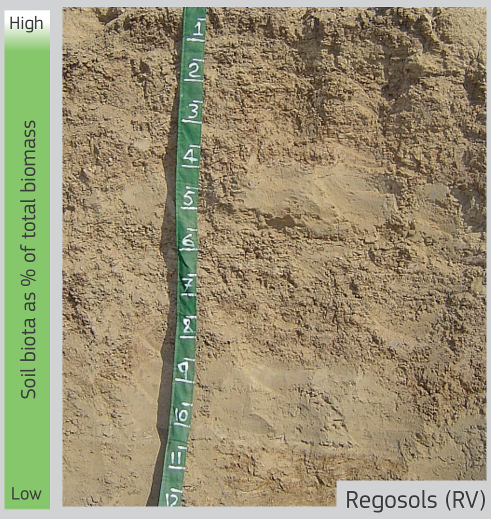


Ornithogenic soils (MBS)

Desert and Dry Shrubland

Soils of this ecoregion are mostly species poor with relatively few faunal species; ants and termites are the most abundant. Soil crusts, dominated by cyanobacteria, are common and include diverse communities of lichens, fungi and bacteria.

Regosols are poorly developed or shallow soils in unconsolidated parent materials with medium to fine textures. Aridity inhibits the development of distinct soil horizons. Organic matter content is low. They can contain significant levels of calcium carbonate or gypsum.



Regosols (RV)

Bars indicating proportion of soil biota in the total biomass of each region are based on compilations of expert judgements.

Soil biodiversity and ecoregions – Tropical and subtropical forest

Wet, moist and woody

Tropical forests can be found in Asia, Australia, Africa, South America, Central America, Mexico and on many of the Pacific, Caribbean and Indian Ocean Islands. Tropical rainforests can be characterised in two words: hot and wet. Mean monthly temperatures exceed 18 °C during all months. Average annual rainfall is not less than 250 mm and can exceed 1 000 mm.

Tropical rainforests exhibit high levels of biodiversity. Between 40 % and 75 % of all biotic species are indigenous to rainforests. Rainforests are home to half of all animal and plant species on the Earth. Two-thirds of all flowering plants can be found in rainforests. A single hectare of rainforest may contain 42 000 different species of insects and up to 1 500 species of higher plants. Rainforests are divided into different layers, with vegetation organised in a vertical pattern from the top of the soil to the canopy. Each layer has a unique biotic community containing animals adapted for life in that particular layer. Four layers are distinguishable:

1. the forest floor, the bottom-most layer, receives only 2 % of sunlight
2. the understory layer lies between the canopy and the forest floor
3. the canopy layer is the primary layer of the forest forming a roof over the two remaining layers
4. the emergent layer is unique to tropical rainforests, while the others are also found in temperate forests. It contains a small number of very large trees, called emergents, which grow above the general canopy, reaching heights of 45 - 55 m; although, occasionally, a few species will grow to a hight of 70 - 80 m

Soil biodiversity occupies the litter layer of the forest floor. Like soil itself, soil biodiversity is strongly related to properties of upper layers.

Aerial view of the Amazon rainforest in Brazil. About half of the world's tropical rainforests are in South and Central American countries. (NP/CIAT)

Unique soil biodiversity of tropical forests: (**a**) a giant earthworm and (**b**) a tailless whip scorpion, both from Ecuador. (GA, GW)

Soil biodiversity

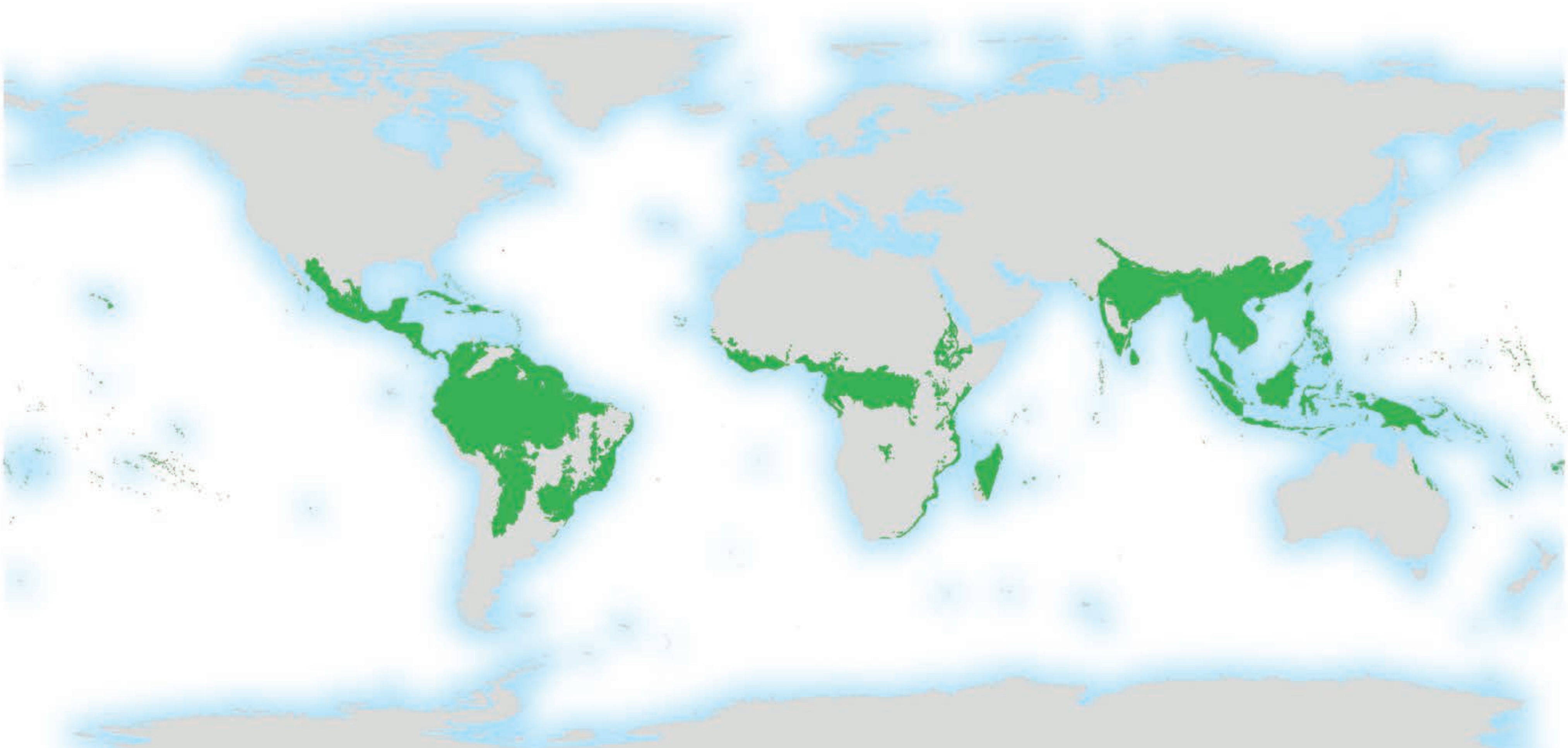
Tropical rainforests host most of global biodiversity as well as most of the recognised biodiversity hotspots worldwide. The numbers of organisms found in tropical soils are huge. For example, studies of soil invertebrate communities have shown the existence of a peak in species richness for oribatid mites, ants, collembolans and termites (see Chapter II). Although basic information is still lacking on species diversity for many other taxonomic groups, the existence of such abundance suggests that tropical ecosystems may host the main part of soil invertebrate biodiversity. [102]

In addition, tropical forests host a wide diversity of invertebrates that are rare or absent from any other biome; for example, tailless whip scorpions (order Amblypygi) and whip scorpions (Uropygi), some of which represent very ancient groups that may have found an ultimate refuge in this kind of environment. The occurrence of giant earthworms is another characteristic of tropical soils. Of course, even small earthworm species are present. Earthworms are more abundant in humid areas and are also sensitive to the nutrient status and organic contents of soils. Communities dominated by litter-feeders are associated with poor soils from South America and Africa, whereas geophagous organisms (i.e. that feed on soil) are characteristic of the rich, neutral soils of Mexico.

Social insects are the most abundant and diverse components of soil invertebrate communities in tropical forests. Tropical forests of Amazonia, for example, may host more than a hundred species at a single location, with all possible functions observed. The impact of termites is more variable and mainly depends on the relative proportions of different functional groups. While humivores (i.e. feeding on humus) and lignivores (i.e. feeding on wood) seem to be present everywhere, possibly with greater diversity in tropical America, fungi-growing species are only found in Africa and some parts of Asia. Fungus-growing termites and ants (see pages 54-55) are among the most impressive examples of coevolution in the world. They can build impressive and long-term nests containing millions of workers, and the agricultural symbiosis with fungi has allowed them to occupy previously inaccessible niches that have abundant resources.

(**a**) A fungus of the genus *Termitomyces* attached to a (**b**) termite fungus farm. Fungal white lumps are almost ready for harvest. (AH)

The surface of tropical soils are characterised by large amounts of decaying material (i.e. plant and animal waste) that support great numbers of fungal diversity. Through DNA-based analysis (see pages 64-65), about 1 700 different species were identified across three major tropical forests in the western Amazon Basin. Distribution of fungi varies not only at spatial but also at temporal scales because of the disturbances caused by seasonal changes in rainfall. Furthermore, it has been shown that pathogenic fungi (see box on page 39) may have a positive effect on plant biodiversity in tropical forests, by acting as a sort of diversity police. Indeed, these fungi spread quickly between closely packed plants of the same species, preventing them from dominating and enabling a wider range of species to flourish.



Global distribution of tropical forests. The map was created by including four recognised ecoregions from the World Wildlife Fund's (WWF) Global Ecoregions database: 1) tropical and subtropical moist broadleaf forests, 2) tropical and subtropical dry broadleaf forests, 3) tropical and subtropical coniferous forests and 4) mangroves (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity and ecoregions – Temperate and boreal coniferous forest

Cold, woody and acid

Coniferous forests are made up of cone-bearing trees whose leaves are small, mostly evergreen, needle- or scale-like. They are extensive in the northern hemisphere (they also occur, to a lesser extent, in the southern hemisphere but their distribution is not visible given the scale of the map below). Boreal coniferous forests are found between 50 °N to 70 °N and are conditioned by long dry, cold winters and short, warm summers. Temperate evergreen forests are common in the coastal areas that have mild winters and heavy rainfall, or inland in drier climates or montane areas. Temperate conifer forests sustain the highest levels of biomass of any terrestrial ecosystem and are notable for the massive proportions of trees in temperate rainforests. The dominant tree species of the boreal forests are spruce, pine, fir and larch, while cedar and redwood are characteristic additions in temperate regions.

Soils in coniferous forests are often podzolic (see box on page 21) due to the acidic litter, and characterised by the leaching of nutrients downwards into lower soil horizons. The litter layer is composed of acidic and dry needles and fallen twigs, which decompose very slowly. Forest soils take around 1 000 years to form a 25 mm soil layer. The acidic forest soils also shape the habitats of soil organisms, and the largest organism group (by biomass) in boreal forests is fungi. There can be several thousands of metres of hyphae in one gramme of soil, and fungal hyphae can extend over large distances. Fungi are important in forests as they produce extracellular enzymes that can decompose woody material and degrade both lignin and cellulose. The diversity of fungi and their different enzyme production enables the turnover of carbon and other nutrients in forests soils.

In coniferous forests, (**a**) the ant *Formica rufa* builds (**b**) nests in the form of mounds of leaves and pine needles. (DE, OBI)

Boreal forest in Sweden. Also known as taiga, boreal forests consist of coniferous trees, mainly pines, spruces and larches. (ABA)

Soil biodiversity

Coniferous forest soils contain a wide range of animals ranging in size from nematodes (see pages 46-47) to enchytraeids and ants (see pages 48, 54). The largest groups are enchytraeids and earthworms, followed by mites, spiders, beetles, nematodes, collembolans, protists, rotifers and dipteran larvae (see Chapter II). Nest-building ants are common and can form large colonies, using the pine and spruce needles for nest building. In the boreal forests of Europe, the enchytraeid species *Cognettia sphagnetorum* can make up 80 - 90 % of the enchytraeid numbers and biomass, and can be the dominant soil animal species in terms of overall biomass. Because of the acidic conditions in the uppermost soil, acid-sensitive soil animals, such as burrowing earthworms, are normally scarce or absent. The acid tolerant earthworm *Dendrobaena octahedra* may contribute significantly to the soil animal biomass, but occur usually in productive forests and at more southern latitudes. [103]

Several fungi can be found in coniferous forests. Many of them live in symbiosis with trees, such as this *Sarcodon imbricatus*. (SL)

Food webs in coniferous forests are dominated by fungi, and soil fauna has a much smaller biomass in food webs. However, when considering the different parts of the food webs in terms of functions such as decomposition, the soil fauna has a larger impact on carbon and nitrogen cycling than their biomass indicates. The number of organisms and their part in the food web can thus influence the decomposition rate of organic matter. Furthermore, natural or human-caused changes in the forest ecosystem can influence ecosystem functions.

The most abundant mycorrhizae in boreal forests are the symbioses between trees, such as spruce and pine, and ectomycorrhizal fungi (see page 40). Coniferous forest trees are highly dependent on their fungal partners, and symbioses contribute greatly to tree growth. Ectomycorrhizal fungi also protect trees from parasites, predators, nematodes and other soil pathogens. Ectomycorrhizal fungi are important for the storage of carbon in soils, and it has been estimated that 10 - 50 % of all the carbon assimilated by the trees is translocated into fungal hyphae. More than half of the carbon stored in the soil originates from roots and mycorrhizae and, therefore, on a global scale the boreal forest soils are large carbon sinks, driven by ectomycorrhizal fungi.

Global distribution of boreal (also known as taiga) and temperate coniferous forests. The map was designed by including two recognised ecoregions from the World Wildlife Fund's (WWF) Global Ecoregions database: 1) boreal forests/taiga and 2) temperate conifer forests (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity and ecoregions – Temperate broadleaf and mixed forest

Moderate, woody and rich in litter

Temperate forests occur in areas with distinct warm and cool seasons, which give them a moderate annual average temperature (3 to 16 °C). About 570 million hectares are covered by temperate forests, making it one of the major ecoregions on Earth. This biome plays a crucial role in the global carbon budget. In this ecosystem, carbon (C) enters the soil in the form of plant litter through the belowground allocation of C thats has been fixed by plant photosynthesis (see box on page 35), and as dead fungal and animal material. As a consequence of the input of new litter (leaves, dead wood) and its transformation, it is possible to recognise three distinct layers in the soil profile:

- the litter (L horizon – see page 10), composed of organic matter derived, almost exclusively, from dead plant biomass
- the organic (or humic) H horizon: representing a mixture of processed plant-derived organic matter and soil components
- the mineral soil horizon: originating both from the decomposition of organic matter and exudation from the abundant tree roots.

Compared to other ecosystems, forest specificity lies in the presence of dead wood material. Dead wood represents between 10 and 20% of plant biomass in these forests. Moreover, it has been estimated that dead wood material (e.g. fine or coarse woody debris) comprises about 18 % of the carbon stock in temperate forests. The great presence of woody material influences the communities of soil organisms.

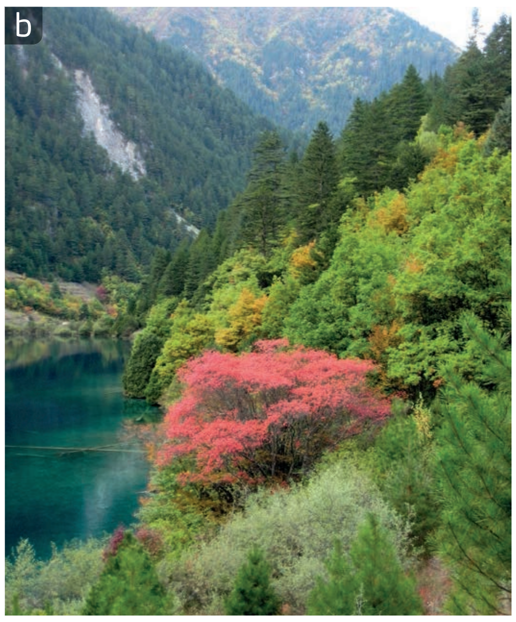
In temperate forests, many beetles, such as this woodboring beetle (*Chrysobothris* sp.), have a diet that consists primarily of wood. (KS)

Soil biodiversity

Soil biodiversity in temperate forests shows a high abundance of decomposers. The diverse assemblage of arthropods associated with dead wood are known to accelerate decomposition. Various processes could take place during the whole process (e.g. consuming and excavating wood, hastening wood fragmentation through mechanical weakening, and facilitating fungal colonisation through tunnelling). The relative importance of each process varies greatly depending on wood traits, faunal composition and abiotic conditions (e.g. temperature, humidity, resource quality, etc.). By contrast, termites (see page 55) are concentrated in warmer regions, and beetles (see page 59) associated with dead and dying wood are distributed much more widely. During the decomposition process, changes in wood characteristics impact the total abundance of millipedes and isopods (see pages 56-57), with their number increasing as wood density decreases. [104]

In temperate forests, the soil community also includes microorganisms. Fungi, particularly the basidiomycetes (see pages 38-39), are the main microorganisms responsible for wood decomposition because of their ability to degrade recalcitrant ligno-cellulose complexes. Fungi that help wood decay can be broadly categorised into primary, secondary and end-stage colonisers:

- primary colonisers are present as spores in the standing trees. They proliferate through the uncolonised wood, utilising easily accessible nutrient sources and then more recalcitrant compounds
- secondary colonisers are present as spores, but also arrive as mycelium that has grown out of colonised resources looking for new substrates
- end-stage fungi proliferate as they can tolerate certain environmental stresses; they are not able to compete for substrates used by primary and secondary colonisers.



(**a**) A temperate birch forest in Colorado (USA) and (**b**) the most biologically diverse temperate forest in the world in Jiuzhaigou Valley (China). Main characteristics of these forests include: broad leaves, large and tall trees and no seasonal vegetation. (YS, RD)

Fungi are the main wood decomposers in temperate forests. (GI)

Global distribution of temperate forests. The map was created by including only ecoregions from the World Wildlife Fund's (WWF) Global Ecoregions database: temperate broadleaf and mixed forests (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity and ecoregions – Temperate grassland

Seasonal and grassy

Temperate grasslands are located north of the Tropic of Cancer and south of the Tropic of Capricorn. The main temperate grasslands include the pampas of South America, the steppes of Eurasia and the plains of North America. Due to aridity, they are generally desert in Africa (see page 87). Grasslands cover extensive areas, comprising approximately 40 % of the Earth's terrestrial surface, thus making them one of the most successful vegetation types on the planet.

There are different grassland types usually split into three broad groups: temperate, tropical (also known as savannah – see page 82) and montane (see page 84) grasslands. Perennial grasses are dominant; with their growth buds at or just below the surface, they are well-adapted to drought, fire and cold. The tiller, or narrow upright stem, reduces heat gain in the hot summers; the intricate root systems trap moisture. Temperate grasslands have warm summers and severe winters. Snow often serves as a reservoir of moisture for the beginning of the growing season. Seasonal drought and occasional fires help maintain these grasslands, which have played an important part in human history.

As well as being used for grazing livestock since animals were first domesticated over 7 000 years ago, many of our commercial grains, such as wheat and barley, were almost certainly first domesticated from wild grasslands. Further distinctions can be made to include the high-altitude grasslands (i.e. montane grasslands), and even between natural (or native) grasslands and secondary grasslands, that derive from a recolonisation of herbaceous plants after human-induced modification. Grasslands generally have relatively deep soils that are rich in nutrients due to large amounts of tissue dying off each year, which builds up in the organic matter portion of the soil. Relatively few 'natural' grasslands remain as most have been turned into farms or are used for grazing livestock.

(**a**) A grassland in Patagonia, Chile and (**b**) the Hulun Buir grasslands in Mongolia, China. The predominant vegetation of grasslands consists of grasses and/or shrubs. (DSC, LL)

Soil biodiversity

The amount of life found below the surface of grasslands dramatically exceeds that found aboveground, in both number and mass, as well as species richness, and is particularly rich even when compared to other belowground environments. [105]

Grasslands are unique compared to virtually all other biomes in that they have a relatively simple structure but very high levels of species richness. It has been estimated that there are approximately 100 tonnes per hectare of living biomass below the surface of temperate grasslands, consisting of bacteria, fungi, earthworms, microarthropods and insect larvae. The majority of grasslands are managed to some extent, whether through grazing, mowing or by planting specific species of grass for a particular purpose, such as for forage or improved pasture.

Being rich in earthworms and other soil fauna, temperate grasslands are also home to moles. Unfortunately, there appears to be no simple formula for calculating the mole population from the number of molehills. (CB)

A common feature of less managed, species-rich grasslands is that they have fungal-based food webs, contrary to more intensively managed grasslands that have bacterial-based food webs. Arbuscular mycorrhizal fungi (AMF – see page 40) are a common component of grassland ecosystems, where they can influence plant productivity, plant diversity, and plant defense to herbivory and soil stability. Researchers report that the number of AMF species in temperate grasslands ranges from 10 to 24, thus representing one of the most diverse ecosystems in terms of this group of soil organisms. It is well known that plant diversity increases significantly with increasing AMF-species richness. Furthermore, it has been demonstrated that grazing (see pages 124-125) decreases AMF spore abundance but increases AMF-species richness.

The presence of grazers may also influence other soil communities: 144 species of arthropods from cow dung were recorded in a temperate grassland. Earthworms (see page 58) are also very abundant in grasslands. Soil fauna data show that they form the greatest biomass (70 - 80 % of the total) of temperate grassland animals. Such an abundance has clear effects; it was found that 30 % of grass seedlings germinate from earthworm casts. This indicates that earthworm casts increase the spatial heterogeneity of grassland plant communities. Grasslands are also often home to moles (see pages 62-63). The number of mole hills is not a measure of the number of moles in a given area. In order to estimate the number of moles, the total surface of the dug area must be taken into account. It has been calculated that the territory of a mole is about 3 000 square metres for males (up to 7 000 square metres in the breeding season) and about 2 000 square metres for females.

Global distribution of grasslands. The map was designed by including recognised ecoregions of the Global Ecoregions database of World Wildlife Fund (WWF): temperate grasslands, savannahs and shrublands (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity and ecoregions – Tropical and subtropical grassland

Grassy, dry and burnt

Tropical and subtropical grasslands, also known as savannahs, are distinguished by a warm and dry climate compared to temperate grasslands, as well as the occurrence of seasonal droughts. Savannahs are amongst the most complex and variable biomes on Earth and are difficult to define precisely. Nevertheless, a number of characteristics define savannahs throughout the world: 1) a continuous or near-complete cover of a mostly grassy herbaceous stratum, with tree and shrub strata varying from a total canopy cover (savannah woodland) to open grassland; 2) marked seasonal contrasts with periodic or annual fires typical of dry seasons, lasting anything from two to nine months; 3) underlain by mostly nutrient-poor soils, prone to desiccation in the dry season and inundated in the rainy season.

The vegetation consists of mixtures of trees, shrubs, grasses and ground plants, but the proportion of these components can change rapidly from place to place and over time. Animal life above- and belowground may show equal diversity. Savannahs are globally distributed almost entirely within the Tropical Belt. There are significant continental differences, with the Australian savannahs generally having the driest and the South American the wettest climatic environments. The African savannah is the most well-known, characterised by grassy landscapes and mixed communities of trees, shrubs and grasses with large grazing mammals.

Soil biodiversity of African savannahs

About 40 % of the arable lands south of the Sahara desert are savannahs, characterised by two very contrasting seasons: dry and wet, with a variable average annual rainfall. The African savannah is a thornbush savannah, which has many different kinds of plants, such as Acacia trees, Candelabra trees, Jackalberry trees, Umbrella Thorn Acacias, Whistling Thorns, Bermuda grass, Baobab trees and Elephant grass. The soils (Cambisols, Ferralsols and Lixisols – see pages 26-27) are usually well drained and contain little organic matter. In West Africa, soil is managed by alternating crops, such as millet, sorghum and groundnuts, and fallow. This practice affects the activity and diversity of soil organisms. [106]

A large variation in the total density of macrofauna (ants, termites and earthworms) is possible, the most abundant groups being ants and termites (see pages 54-55). The density of termites increases with the age of the fallow. The abundance of functional groups within the various taxonomic groups is even more variable. For example, endogeic earthworms (see page 58) appear to be most abundant in 10-year-old fallow, although they tend to be less abundant in fallows older than 30 years. However, epigeic earthworms that live in and feed mainly on litter are more abundant in older than in the younger fallows. Fungus-growing termites, such as the species *Microtermes hollandei*, are most abundant in short-term fallows, whereas humivorous (feeding on humus) species, such as *Ancistrotermes crucifer*, are found more frequently in long-term fallows. Regarding microfauna, various studies carried out in Senegal have shown that there is no significant difference between the total number of nematodes (see pages 46-47) in cultivated and fallow land. However, the diversity of species increases with the age of the fallow.

Diversity of fires and termites

- One of the factors characteristic of all savannah environments is wildfires in the dry season.
- Fire is an important disturbance in African savannahs.
- It has been hypothesised (pyrodiversity-biodiversity hypothesis) that high levels of pyrodiversity (season and frequency of fires) are necessary to maintain high levels of biodiversity.
- Research has shown very little species density and occurrence of termites across the different fire regimes.
- Therefore, for termite control there is only limited support for the pyrodiversity-biodiversity hypothesis.

A nest of termites surrounded by fire in Africa. Wildfires do not impact the overall diversity of these soil organisms. (JBD)

For example, plant pathogenic species, such as *Scutellonema cavenessi*, dominant in cultivated fields, persist in long-term fallows, but are significantly reduced. The total microbial biomass (bacteria and fungi – see pages 33-35, 38-41) is low and not significantly different in cultivated fields and in fallows. However, the characterisation of the functional diversity showed that the microbial functional profiles were more diversified in fallows than in cultivated fields. In fallows, mycorrhizal fungi (see page 40) of the genus *Glomus* are the most abundant.

Savannah is a grassland ecosystem characterised by widely spaced trees to avoid closed canopy conditions. (**a**) Termite mounds in the Australian savannah, one of the typical soil-living organisms in these areas. (**b**) In African savannah the dry season lasts more than seven months per year. (**c**) *Cerrado* accounts for about 20 % of Brazil's land surface. (PMO, CJM, ON)

Global distribution of savannahs. The map was developed from the Global Ecoregions database of World Wildlife Fund (WWF). Savannahs cover approximately 20 % of the Earth's land area. This map was designed by including two recognised ecoregions: 1) tropical and subtropical grasslands, savannahs and shrubland and 2) flooded grasslands and savannahs (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity and ecoregions – Mediterranean forest, woodland and shrubland

Patchy, hot and rainy

Mediterranean environments include forest, shrubland, grassland and 'badland' (including arid and semi-arid) habitats, with some exceptions. In fact, the combination of many adjacent habitats gives Mediterranean landscapes a distinctive transitional as well as patchy structure, which results in a characteristic diversity of plant and animal populations. Five regions in the world are considered Mediterranean-type ecosystems; the Mediterranean Basin, central Chile, southern and central California, the Cape Province of South Africa and two parts of southern Australia in the centre and the west. Similar climate patterns, with dry and hot summers and rainy winters and the common proximity of marine and arid biomes, provoke clear cases of species convergence. However, a different biogeography and history of disturbances (principally fire and land exploitation) generate differences at the community level among these areas.

Soil types vary among regions due principally to differences in the underlining parent material; in the Mediterranean Basin this is basically limestone, which is reduced to strips in South Africa and Australia, and does not exist in Chile and California. In any case, due to the strong seasonal contrast, Mediterranean soils share a modest profile development, which tends to decrease with increasing elevation. All regions present a mosaic of old and newer soils, showing a general scarcity of nutrients and low water content. This mosaic is accentuated due to the formation of 'fertility islands', created by trees, shrubs or even faunal structures, such as ant mounds, in a matrix of almost bare soil. In these islands, plant structure and resources and the biology of the associated soil fauna create very different soil microhabitat conditions between the islands and the matrix and among different types of islands. In general, litter and soil compartments are much more differentiated than in other ecosystems, and the tenuous intermediate phase between them gets thinner from mesic to arid environments.

Although there is a common resemblance among aboveground plant parts such as evergreen plants, root systems are more variable depending on soil and rock conditions. Some widespread adaptations of roots to desiccation and the lack of nutrients in Mediterranean-type ecosystems are: the persistence of the primary root, deep penetrating roots in woody plants while the roots of some succulent plants extend horizontally over wide areas, seasonal variations in the vertical root structure by root contraction or fine-root turnover, and associations with actinobacteria (that form root nodules – see box on page 99) and mycorrhizal fungi (see page 40). In fact, mycorrhizae have been mentioned in numerous studies as being crucial components of the root system in Mediterranean ecosystems, especially in semi-arid and arid environments. Another important structural component of some Mediterranean soils is the existence of biological soil crusts (see page 73), which seem to play a fundamental role in soil resistance to erosion.

Oak woodlands are characteristic of the Mediterranean Basin and California. (SMA)

Global distribution of Mediterranean forests, woodlands and scrubs. The map was created from the World Wildlife Fund's (WWF) Global Ecoregions database: Mediterranean forests, woodlands and scrubs (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity

Microbial communities are principally associated with the rhizosphere (see page 43) and are subjected to seasonal variations in density. Microbiological activity, including carbon emissions (see page 102), is overall low. Both bacterial and fungal communities (see pages 33-35, 38-41) show great differences among litter and soil levels, while seasonal variations in community structure are higher in the litter layer than in the mineral soil. The bacterial-to-fungal proportion decreases with increasing aridity, indicating the important role of fungi in the decomposition process of Mediterranean-type ecosystems. Belowground fungal communities are very diverse, characterised by a few common types and a large number of rare types, and are very different from aboveground communities. [107]

Protists (see pages 36-37), nematodes (see pages 46-47) and other microfauna are also common in Mediterranean soils. However, microfauna is commonly associated with the soil water fraction. Therefore, Mediterranean ecosystems are not the most suitable environments for this category of organisms. Nevertheless, most microfauna have the ability to develop structures that are resistant to drought (e.g. cysts of nematodes). In this context, general statements are not possible because of the considerable lack of studies on this faunal category in Mediterranean-type ecosystems. An exception could be made for nematodes in the Mediterranean Basin, where they are considered as valuable bioindicators (see page 101) of soil quality.

A larva of the darkling beetle *Zophobas morio*. These larvae are commonly known as superworms and can be found in oak woodlands. Darkling beetle larvae migrate from litter to deeper soil layers. This migration affects the food web as they are eaten by lizards, turtles, frogs, salamanders and birds. (BG)

Meso- and macrofauna are well studied soil animal groups, and data are available, also at a global scale, on their abundance, diversity. Again seasonality, patch distribution and a deep vertical stratification are common features, although vertical migration is a strategy against drought only shared by this group. Insect (e.g. Coleoptera – see page 59) and centipede (see page 57) larvae have been described as very important interconnectors between litter and soil compartments. Among them, the darkling beetle (Tenebrionidae) larvae show significant seasonal migrations, which can change the soil food web structure.

In relation to microarthropods, the five Mediterranean regions share a generally greater abundance of mites than collembolans (see pages 49-50), due to their high dependence on soil moisture. Among mites, Oribatida are mainly detritivores, and Prostigmata are predators in Mediterranean environments and, therefore, their diversity has important impacts on ecosystem functioning.

Among soil macroinvertebrates, there are different ecosystem engineers (participating in decomposition processes and soil aeration, drainage and bioturbation) for different habitats. Earthworms (see page 58) are the soil burrowers of more humid forests, while beetle larvae dig through bad land soils. Other detritivores of Mediterranean type ecosystems are isopods and millipedes (see pages 56-57). Ants (see page 54) and dung beetles (see page 59) also actively participate in the cycling of organic matter by distributing it among patches and from the surface to deeper soil levels, thus playing the role of termites in tropical ecosystems. An interesting adaptation to belowground patchiness is that of the insects known as ground pearls (genus *Margarodes*), which can develop as root-feeding pests in almost all Mediterranean regions. Active burrowing by herbivores is represented by Curculionidae and scarabaeid larvae (see page 60). Ground beetles, which perform an important role as soil predators, are also typical of the Mediterranean region. They are accompanied by beetles, centipedes, arachnids (see page 61) and pseudoscorpions (see page 53). This last group of arthropods has been subjected to a biogeographical comparison due to their representativeness, wide distribution and available information. Results show that affinities are greater among Mediterranean areas in the same hemisphere than between North and South. In this sense, similarities are greater in America than between the Mediterranean Basin and South Africa.

Different Mediterranean vertebrates, principally mammals but also some sea birds, affect soil fauna by fertilising, digging, burrowing and compacting the soil, but only a few species can be considered truly subterranean. Among them, the Middle East blind mole-rat, a voracious herbivore, and worm lizards (see page 63), small predators, are exclusively from the Mediterranean Basin.

A specimen belonging to the genus *Margarodes* (Hemiptera), commonly known as ground pearls. Ground pearls excrete a waxy covering that completely surrounds their body, apart from their piercing-sucking mouthparts. The waxy spherical covering of the insect is the structure most likely to be encountered. The sphere is pink to yellowish-brown and resembles a pearl. The exposed mouthparts are used to feed on and attach to plant roots. (MBE)

Soil biodiversity and ecoregions – Montane grassland and shrubland

High altitude and unique species

Montane grasslands and shrublands located above the tree line are commonly known as alpine tundra, and occur in mountainous regions around the world. This major habitat type includes the Puna and Páramo in South America, subalpine heath in New Guinea and East Africa, and the steppes of the Tibetan Plateau. Montane grasslands and shrublands, particularly in subtropical and tropical regions, often evolved as virtual islands, separated from other montane regions by warmer, lower elevation regions, and are frequently home to many distinctive and endemic plants (i.e. characteristic of a specific place) which evolved in response to the cool, wet climate and abundant tropical sunlight.

The páramos of the northern Andes are the most extensive examples of this habitat type. The heathlands and moorlands of East Africa (e.g. Mount Kilimanjaro, Mount Kenya, Rwenzori Mountains), Mount Kinabalu of Borneo and the Central Range of New Guinea are all limited in extent, extremely isolated, and support highly endemic biodiversity. Drier, yet distinctive, subtropical montane grasslands are found in the Ethiopian Highlands, Zambia and southeastern Africa. A unique feature of many alpine grasslands is the presence of distinctive plant species, such as *Lobelia* spp. (Africa) and *Puya* spp. (South America). Montane grasslands form where sediments from the weathering of rocks (see page 20) have produced soils that are sufficiently well-developed to support grasses and sedges. Because of the elevation, in some areas, such as the highest zones of the Tibetan Plateau, plants are not able to grow and the soil is covered by a biological soil crust (see page 73). Of course, such peculiarities may have an influence on soil-living organisms.

Puya alpestris is a plant native to the Chilean Andes. The unique plant communities influence soil biodiversity in montane grasslands. (PN)

Montane grasslands are fragile habitats, exposed to several pressures due to their challenging climatic and soil conditions. Excessive ploughing, overgrazing, burning (see Chapter V) and growing populations are especially evident. In particular, the activity that has the greatest negative impact on montane habitats is overgrazing. This leads to modifications of the vegetation structure and alteration of soil biodiversity associated with those plant species. In extreme cases, very heavy grazing and trampling can lead to exposure of bare soil and erosion (see pages 128-129), with a possible further reduction of soil life. Because of their distribution and relatively limited accessibility, soil biodiversity in alpine grasslands has not been extensively investigated. However, it is possible to find some interesting case studies.

Montane grasslands from all over the world: (**a**) Páramo in Colombia and (**b**) Drakensberg (meaning 'Dragon Mountains') in South Africa. (MCL, AY)

Soil biodiversity

Most studies on soil biodiversity in montane grasslands have been conducted in the Tibetan Plateau. For instance, about 30 arbuscular mycorrhizal fungal species (see page 40) were isolated in two different analyses. Soil biocrust from the Tibetan Plateau was also analysed, and an increase of the cyanobacterial (see page 35) biomass was observed with increasing elevation. The soil microfauna of Tibetan grasslands was also studied. A study of nematode communities along a grazing gradient, from low to high intensity, retrieved a total of 37 genera with, interestingly, the highest richness in the areas subjected to high levels of disturbance. In particular, nematodes feeding on plants and bacteria (see pages 46-47) were the most well adapted to those conditions [108]. Lastly, a comparison of mite and collembolan communities (see pages 49-50) showed the dominance of mites in the Tibetan meadows.

Tachyoryctes macrocephalus, also known as the giant root-rat or Ethiopian African mole-rat, is a soil-living rodent species present only in the grasslands of the Bale Mountains in Ethiopia. (AT)

A good example of an endemic species is the Ethiopian African mole-rat (*Tachyoryctes macrocephalus*) that lives exclusively in the high plateau of Ethiopia, from 3000 to 4150 m. It is a solitary, aggressive animal living underground in a system of foraging burrows, where it creates a deep nest with a toilet area. The species density is typically 36 individuals per hectare, but reaches 90 individuals/ha when conditions are favourable. It prefers soil depths below 50 cm, and its burrowing activity aids in the aeration and mixing of soil and enhances infiltration of water, thus curtailing erosion. There are also other burrowing rodents endemic of alpine grasslands, such as the Chinese Zorok (*Eospalax fontanierii*) in the Tibetan Plateau. Despite all the presented examples, the spatial and temporal distribution of soil biodiversity in montane grasslands requires further evaluation.

Global distribution of montane grasslands. The map was created including only recognised ecoregions from the World Wildlife Fund's (WWF) Global Ecoregions database: montane grasslands and shrublands (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity and ecoregions – Tundra

Cold, flat and treeless

The word 'tundra' originates from the Saami word *tūndar*, meaning treeless plain. The tundra is a vast, flat, treeless landscape found in the high latitudes surrounding the polar regions, primarily in Alaska, Canada, Russia, Greenland and Fenno-Scandinavia (Finland, Norway, Sweden and parts of Russia). The region's long, dry winters feature months of total darkness and extremely low temperatures. Most precipitation falls in the form of snow during the winter, and soils tend to be acidic and saturated with water when not frozen. Soils are affected by freezing and often have a perennially frozen subsoil, known as permafrost (see page 16). During the summer, the permafrost thaws, but because of the permanently frozen subsoil, the water cannot drain away and soils become waterlogged, forming a distinctive wetland habitat. The tundra can also be found at high altitudes (see page 84) where the soil temperature is below freezing for large parts of the year (and usually at night in the summer).

Vegetation cover is very similar to high-latitude tundra, but soils tend to be well drained. The landscape is generally devoid of trees, because plant growth and survival are limited by short, cold growing seasons, and the lack of suitable substrates and nutrients. Therefore, the vegetation is composed of dwarf shrubs, sedges, grasses and mosses. Due to the harsh climate, tundra has seen little human activity. Nevertheless, some signs of human presence can be found; reindeer herding is one of the most extensive forms of human interactions with tundra ecosystem. Herding and grazing have significant impacts on tundra vegetation and, consequently, on soil-living organisms. Furthermore, these regions are continuously being developed for their natural resources, such as oil and uranium. Therefore, in the past years new settlements have been developing in many parts of Alaska and Russia. Tourism in these remote areas is also expanding. If not carefully managed, this development can lead to the alteration of the environment. Despite all the adverse environmental and human factors, varied communities of organisms are active in tundra soils.

Tundra in Alaska (USA) showing its typical treeless landscape. (WANP)

Tundra is rich in (**a**) lichens and (**b**) fungi. More than 1 700 and 2 600 species of lichens and fungi are present in the Arctic regions, respectively. (AO, AP)

Soil biodiversity

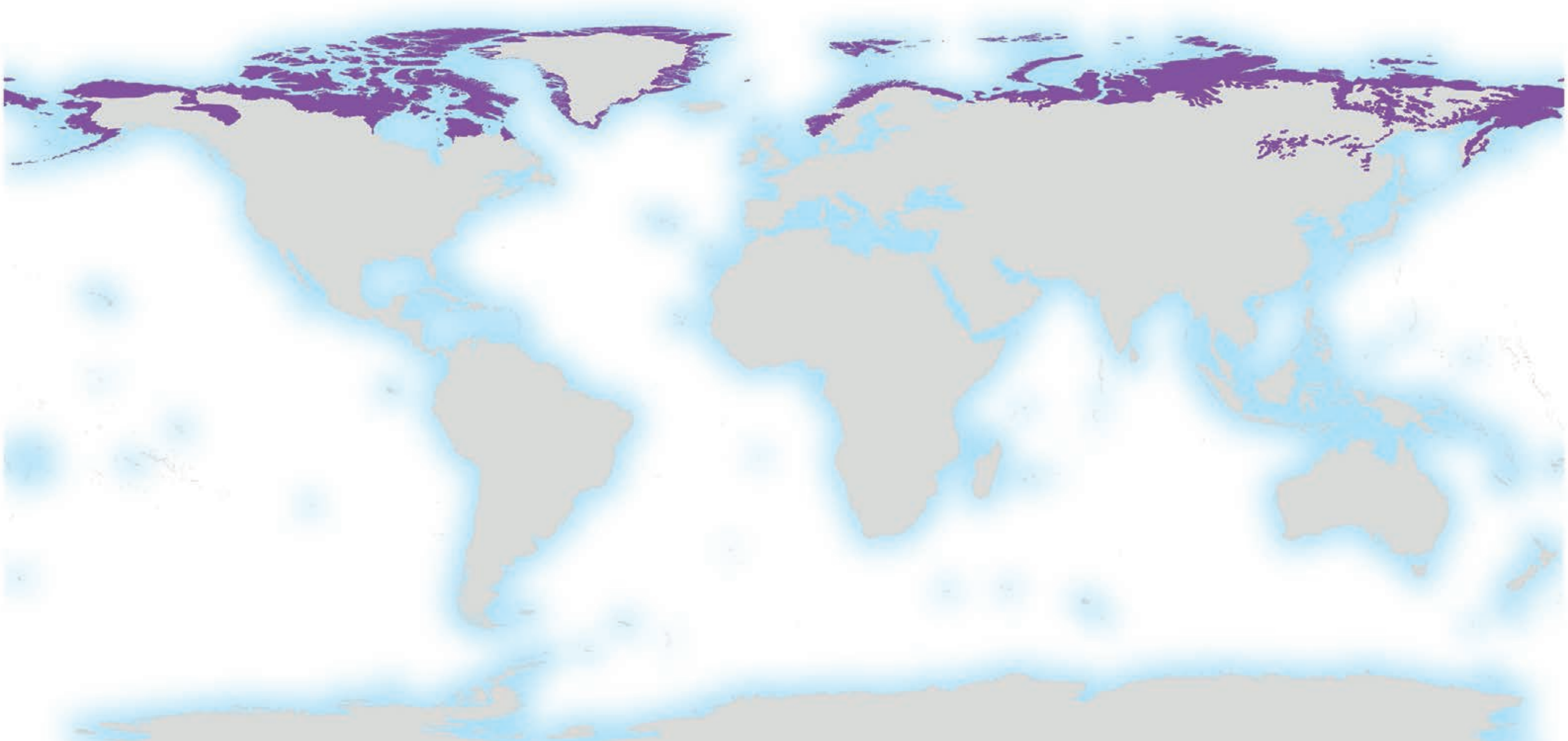
Tundran soil biodiversity is strongly influenced by physical characteristics, such as the extreme seasonality (short cool summers and long cold winters) and the presence of permafrost. Nevertheless, all main groups of soil organisms can be found in this environment. The Arctic Biodiversity Assessment 2013 evaluated the current status of above- and belowground biodiversity in the Arctic region, thus also taking into account soil-dwelling organisms. Densities of bacteria in tundran soils are lower than in temperate soils, but can still reach substantial numbers. Interestingly, recent DNA-based analyses (see pages 64-65) revealed that, during the transition from a frozen to a thawed (winter-summer) state of soil permafrost, there are rapid shifts in microbial abundances, with an increase in actinobacterial (see page 35) populations. Unfortunately, data on archaea and protists remain limited. [109]

Arctic nunataks

- Nunataks, also known as glacial islands, are parts of mountains or ridges not covered by ice or snow within a glacier. They form islands of land and offer good opportunities to study dispersal and succession as glaciers decrease in size and thickness as a result of climate change. Research on dispersal of arthropods on nunataks in Iceland found that:
  - passive dispersal through wind allows spiders, collembolans and mites to be among the first organisms on the virgin nunatak land;
  - soil invertebrate predators and detritivores, such as spiders, collembolans and prostigmatid mites, are common among the first colonisers and precede the establishment of vascular plants;
  - most invertebrates on young nunataks cannot establish and, instead, contribute toward the soil organic matter pool. Flies comprise the majority of the wind-dispersed invertebrates;
  - the wind-dispersed invertebrates are essential as they become resources and sustain local food webs on seemingly barren land until the plants have enough resources to establish.

The nunatak Húsbóndi emerged about 15 years ago in Iceland. (MI)

Much more is known about the presence and abundance of fungal species in tundran soils. Fungi have evolved physiological mechanisms to maintain activity and growth at low temperatures, even when soils are frozen. It has been estimated that more than 11 000 species of fungi live in the Arctic region. Among them, about 2 600 have been described, belonging to all the main fungal phyla (Ascomycota, Basidiomycota, Glomeromycota, etc. – see pages 38-41). Another group of well-established organisms in the tundra are lichens (see page 42). More than 1 700 species of lichens have been found in this environment. Their distribution is also well known, for example, 231 different species have been reported in Greenland. In addition, more than 73 genera of nematodes, 200 species of tardigrades, 85 species of enchytraeids, 400 species of collembolans, 600 species of mites and two species of earthworms have been described in tundra's soils. In conclusion, despite limited data on soil, there is significant belowground life in the tundra biome.



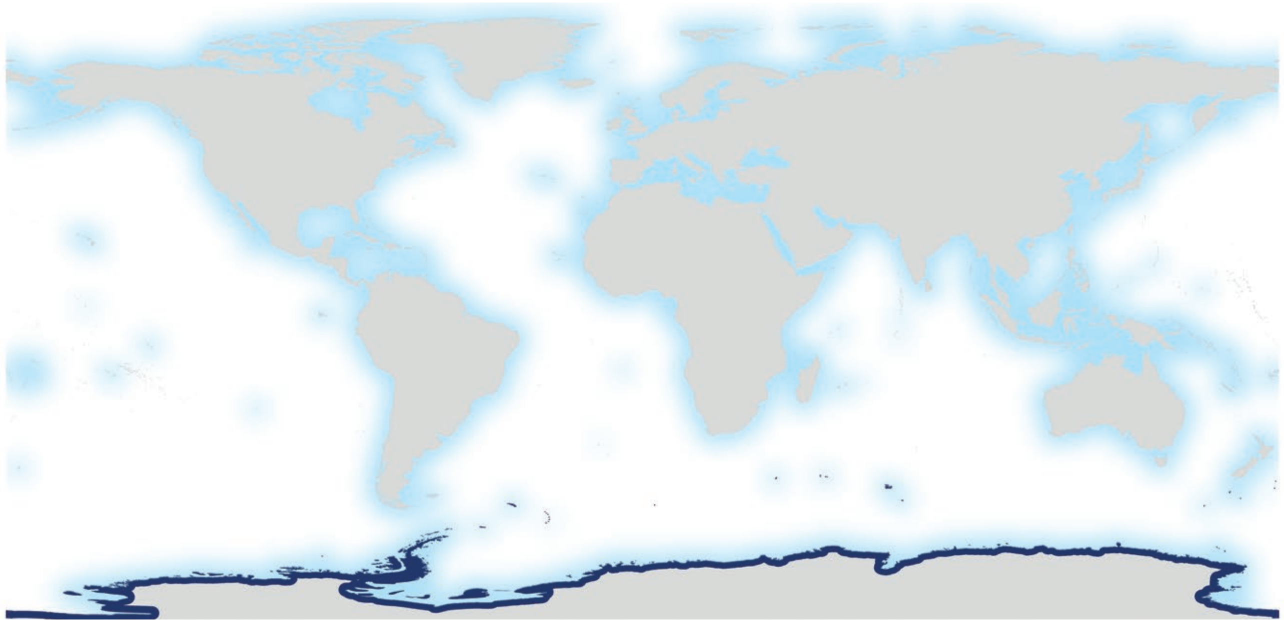
Global distribution of tundra. The map was created including only recognised ecoregions from the World Wildlife Fund's (WWF) Global Ecoregions database: tundra (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity and ecoregions – Antarctica

Cold, dry and extreme

Terrestrial Antarctica is one of the most extreme environments found on Earth. It is a cold and (mostly) dry continent that is effectively isolated from the rest of the world by global weather patterns and the Southern Ocean. Even within Antarctica, patches of habitable soils are highly isolated ranging from small patches (in order of metres) to relatively large extents (several kilometres). Yet, Antarctic soils are anything but uninhabited. It is now known that Antarctica is home to substantial microbial diversity and supports a broad range of common soil fauna, including nematodes, tardigrades, rotifers, mites and collembolans. More than 520 terrestrial invertebrates, of which about 170 are endemic, inhabit Antarctic terrestrial ecosystems. Many of the native organisms are well adapted physiologically to survive and perform critical ecosystem functions, such as biogeochemical cycling under harsh conditions.

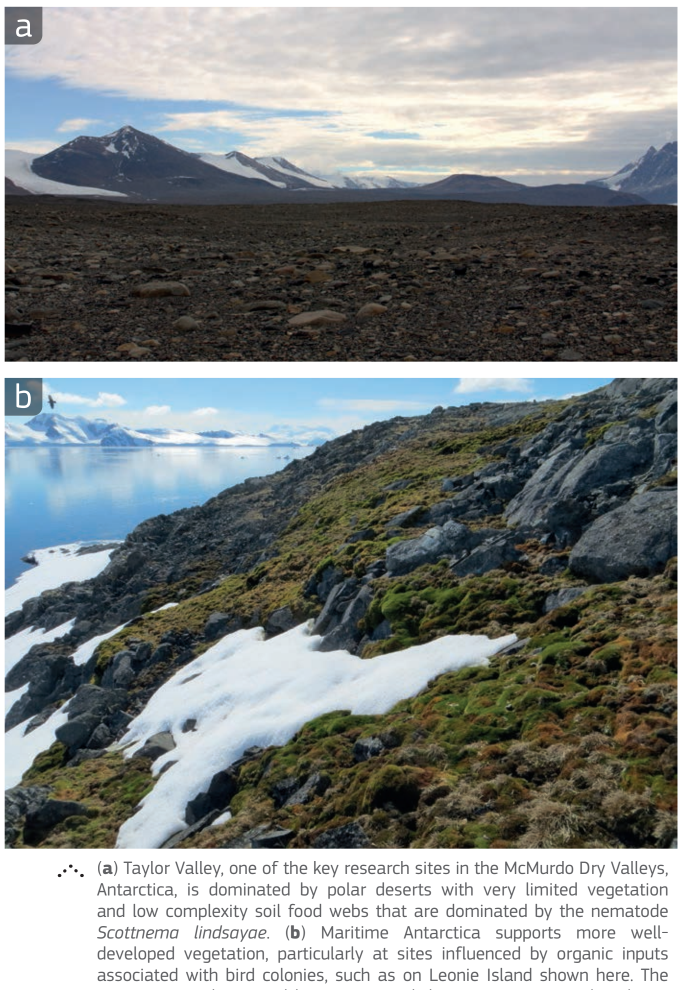
While Antarctic soil systems are in many ways unique, there is much to learn from the diversity and functioning of this extreme environment. They provide, for example, a resource for scientific research into the role of species in ecosystem function, biogeographical patterns, climate change impacts and evolution of life on Earth and, potentially, on other planets. However, solid knowledge of the organisms and communities of terrestrial Antarctica is still lacking, and there is a great need to acquire information on the current diversity and distribution of species within Antarctica and the response and vulnerability of these species to global changes, particularly climate change and human impacts. Here a brief overview is given of the biodiversity of Antarctic terrestrial soil systems and the adaptations that soil fauna have gone through to proliferate in this harsh environment.



The terrestrial Antarctic region. The map shows the coastal portion of the continent, as defined by the World Wildlife Fund's (WWF) Global Ecoregions database, where areas without a permanent ice cover are found (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Soil biodiversity

Antarctica can broadly be divided into three climatic zones: sub-Antarctic, maritime and continental Antarctica. This page focuses on the maritime and continental regions as these represent the most extreme conditions. Colonisation of terrestrial habitats in Antarctica is limited by the Southern Ocean and predominant weather patterns; colonisation events are rare. Therefore, many of the terrestrial inhabitants of Antarctica are endemic species that have survived several glaciation events. Furthermore, the climate,a considerable constraint to the Antarctic fauna and flora, is generally colder than at comparable latitudes in the Northern Hemisphere. Most of continental Antarctica is covered by ice (~ 0.3 % of the land mass is free of snow and ice) and hosts one of the most extreme soil environments with mean annual air temperatures below 0 °C and very limited precipitation compared to the sub-Antarctic islands or maritime Antarctica. [110]



(**a**) Taylor Valley, one of the key research sites in the McMurdo Dry Valleys, Antarctica, is dominated by polar deserts with very limited vegetation and low complexity soil food webs that are dominated by the nematode *Scottnema lindsayae*. (**b**) Maritime Antarctica supports more well-developed vegetation, particularly at sites influenced by organic inputs associated with bird colonies, such as on Leonie Island shown here. The vegetation is dominated by mosses and the two native vascular plants: *Deschampsia antarctica* and *Colobanthus quitensis*. (UNN)

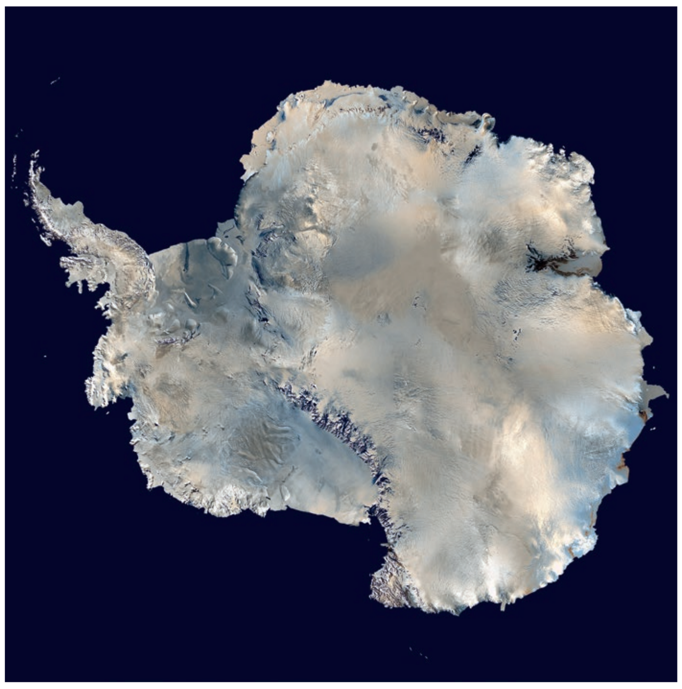
Consequently, the landscape of continental Antarctica is dominated by polar desert ecosystems that support only a few species of mosses, lichen and algae, although more developed vegetation is found in favourable areas along the coastline. By contrast, sites with well-developed vegetation are more common in maritime Antarctica where two native vascular plants also occur (hairgrass, *Deschampsia antarctica*; pearlwort, *Colobanthus quitensis*). Belowground communities are generally simple and highly heterogeneous, with greater biomass and diversity observed in warmer and wetter microhabitats that have vegetated soils and soils impacted by birds and marine mammals supporting the most complex soil food webs. Geothermally active soils represent very distinct microhabitats. Several active volcanoes create geothermally heated soils in an otherwise cold environment and support distinct communities both aboveground (i.e. mosses) and belowground, with several endemic species of bacteria known only from such sites. Importantly, geothermally active soils may have acted as refugia during the last glacial maxima. The diversity of soil invertebrates is relatively low compared with soils in other biomes. Only two higher insects (restricted to maritime Antarctica) and some 225 species of mites, 85 species of collembolans, 49 species of nematodes, 30 species of rotifers and 41 species of tardigrades have been officially recorded.

The species richness of microbial communities is still not well described although recent studies suggest that there is a considerable diversity of bacteria with a high proportion of novel species. Most of the taxa are indigenous and often display psychrotrophic or psychrophilic growth characteristics (see box on page 32), and several genera are unique to Antarctica. Recent advances in molecular tools have provided evidence of an unexpectedly high diversity of microbes in the polar desert of the McMurdo Dry Valleys that was previously thought to support species-poor microbial communities. More than 14 different phyla of bacteria have now been recorded, with the most dominant phyla representing the Acidobacteria, Actinobacteria and Bacteroidetes (see box on page 33). By contrast, the Proteobacteria tend to dominate the soils in maritime Antarctica. Moreover, there is substantial variation in the composition of microbial communities between different regions and landscape types. Therefore, Antarctic soils harbour a high number of novel microbial and animal taxa that contribute significantly to global soil biodiversity.

Adaptations to local conditions

Not only are Antarctic organisms exposed to low water availability and temperatures, they also experience other extreme conditions, such as high salinity and pH values, and even hot soils in the case of geothermally active areas. Many native Antarctic organisms show significant adaptation of growth and survival strategies to survive the severe environmental conditions. Several taxa of Antarctic soil fauna, including nematodes, tardigrades and rotifers, are able to enter a dormant state known as anhydrobiosis that allows them to survive in an ametabolic state for many years during unfavourable environmental conditions (i.e. limited water availability) but also gives protection against other environmental stresses. Tardigrades (see page 44), for example, have been 'revived' from dried plant material after 120 years, and survived being exposed to temperatures near absolute zero as well as several minutes at 151 °C, high pressure and in a vacuum.

Both nematodes and rotifers show similar enhanced capacity to cope with environmental stresses while in the anhydrobiotic state. Other survival techniques include freeze tolerance, as in the case of the chironomid *Belgica antarctica* and the nematode *Panagrolaimus davidi* (the only organism known to be able to survive intracellular freezing), or freeze avoidance as in the case of many microarthropods. Water inside animals generally does not freeze at 0 °C, and significant supercooling can be attained by removing the source of ice nucleation (down to approximately −20 °C). By producing anti-freeze molecules, the freezing point can be lowered even further. Some Antarctic organisms display significant supercooling capabilities. The collembolan *Gomphiocephalus hodgsoni*, for example, has been shown to be able to avoid freezing down to −37 °C under laboratory conditions. To achieve significantly lower freezing points, native Antarctic collembolans generally produce sorbitol and mannitol, whereas mites produce glycerol.



A satellite composite image of Antarctica showing ice covering almost the whole continent (2006). Antarctica is considered to be a desert, with annual precipitation of only 200 mm along the coast and far less inland. The minimum temperature recorded in Antarctica is −89 °C, although the average is −63 °C. There are no permanent human residents, but anywhere from 1 000 to 5 000 people reside throughout the year at the research stations scattered across the continent. Despite these hostile conditions, in the ice-free terrestrial areas soil-living organisms native to Antarctica include many types of bacteria, fungi, plants, protists and certain animals, such as nematodes, tardigrades and mites. (DP)

Antarctic terrestrial ecosystems represent one of the most extreme soil environments on Earth, and are inhabited by a unique collection of species, many of which are found nowhere else on Earth. As many of the native organisms have evolved and adapted to the local environmental conditions they are genetically and functionally distinct from many of the organisms found in what we consider more 'normal' environments. Despite a seemingly low total biodiversity, at least when considering multicellular organisms, this extreme soil environment represents an invaluable pool of novel genes as well as unique functions. Importantly, these endemic species may be highly vulnerable to global change, including climate change, invasive species and direct human impact, given their adaptations to current environmental conditions and limited exposure to disturbances.

Soil biodiversity and ecoregions – Desert and dry shrubland

Hot, dry and hostile

A desert is any region on Earth that can have a moisture deficit lasting the course of a year. Deserts are present on each continent, from the Gibson Desert in Australia to the Thar Desert in Asia, the Sonoran Desert in Mexico and the USA and the Sechura Desert in Peru. They are often regions of extreme temperatures where living conditions are hostile. Deserts vary greatly in the amount of annual rainfall they receive; generally, however, evaporation exceeds rainfall in these ecoregions, usually less than 250 millimetres annually. Temperature variability is also extremely diverse in these regions. Many deserts, such as the Sahara in Africa, are hot all year-round but others, such as Asia's Gobi, become quite cold in winter.

Despite the limited vegetation cover (mainly shrubs) plant diversity can be high. All plants have evolved to minimise water loss; cacti are a representative example of this ability. Desert soils are usually poor because plant growth and productivity is low and the litter layer is almost absent. Furthermore, evaporation tends to accumulate salts at the soil surface.

Soil biodiversity

Soil biodiversity in deserts is lower than in more moist regions, such as temperate forests, but surprisingly, can be higher than in some agricultural ecosystems. The soil surface can be dominated by a soil biocrust (see page 73). The soil fauna is dominated by mites and nematodes (see pages 46-47, 49). As nematodes require water films to be active, much of their time in desert soils is spent in an inactive state. Other abundant microarthropods include collembolans (see page 50) and a wide variety of insect larvae (see page 60). [111]

Concerning the microbial communities, protists (see pages 36-37) are even more abundant than fauna in deserts. Of these, naked amoebae tend to be the most abundant, followed by testate amoebae, ciliates and flagellates. Protists also require water films for activity and, thus, can remain inactive. Unlike more moist regions, where soil biota are more homogeneously distributed because organic matter is more evenly spread, the distribution of soil biota in deserts is more heterogeneous, found clumped together in soils under the canopy of perennial plants, where organic matter is highest.

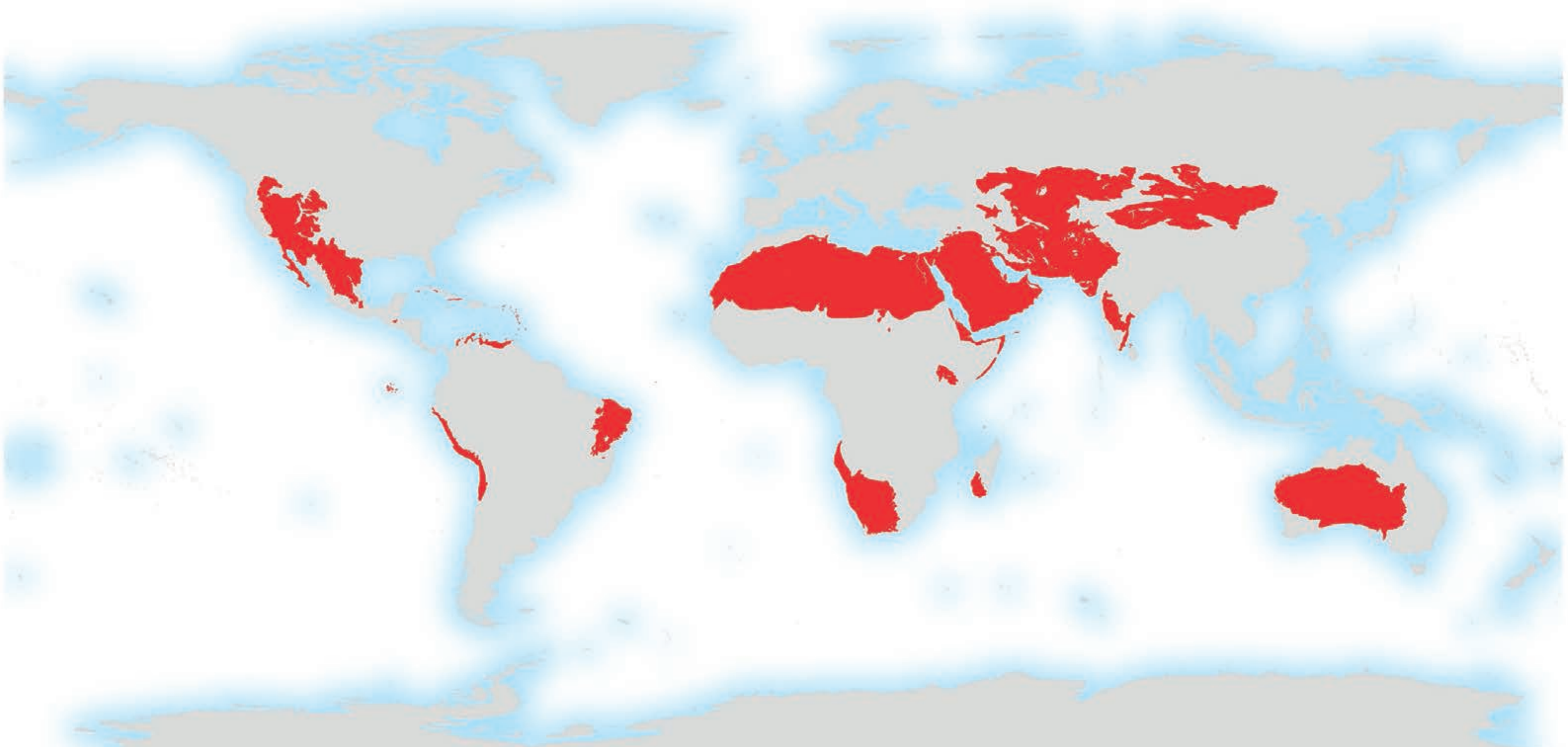
(**a**) In deserts, the living conditions are hostile for plant and animal life because of the environmental conditions. However, many (**b**) plants and (**c**) soil-living organisms are well adapted to these conditions. Among others, in a desert one can find mites, nematodes, ants and termites. (FB, HB, MAL)

However, if interspace soils are covered by a biocrust, soil biota is often more evenly distributed across the landscape. Desert soil communities are critical in driving ecosystem processes, such as nutrient cycling and decomposition (see Chapter IV). Important decomposers in deserts include microorganisms (e.g. bacteria and fungi) and macroorganisms (e.g. mites, collembolans, nematodes, ants, termites, beetles, scorpions and lizards – see Chapter II). Despite the relatively low numbers of soil biota in deserts, they play a critical role in the structure and function of desert ecosystems. The number and biomass of these organisms determine, to a large degree, the rates and overall availability of nutrients for the primary producers (i.e. plants) of the food web (see page 96), and also provide food resources for higher trophic animals (e.g. reptiles and mammals).

Climate and land-use changes represent the main threats to organisms living in desert soils. Higher predicted temperatures will reduce soil moisture and, thus, reduce the overall activity and diversity of soil organisms. If precipitation is concomitantly decreased, further reductions in activity are expected. In addition, the relative proportion of species is likely to change. Human use of deserts is increasing in most areas of the world, with increasing needs for forage, energy and minerals. Many soil organisms are highly sensitive to soil compaction, displacement and movement and, therefore, will be reduced or extirpated by these human disturbances.

Termites and ants

Ecosystems often have a certain species or groups of species that play dominant roles in ecosystem structure and function; this is also the case in deserts. In most arid regions, termites (see page 55) are numerous in species and number. These insects eat and provide food for many other animals. They are especially important in accelerating decomposition and nutrient-cycling rates. Their activities create macropores and they actively drag litter down into the soil, while bringing soils and rocks to the surface. African and Australian termites are the most diverse, whereas North American termites are fairly depauperate. Despite there being only a few species, North American termites still consume most of the plant and dung materials in these deserts compared to other organisms. Ants (see page 54) discard seed coatings and insects carcasses at the mound entrance, further increasing soil fertility. Many species clear vegetation around their nests, thus affecting plant distribution; their mounds, which are up to five metres wide and one metre high, affect local water patterns. Together, harvester ants eat more than 100 species of seeds, but different species often show narrow seed preferences which they usually collect from the soil surface. They are important seed dispersers because they drop many of the seeds they collect. Ant nests also provide refuge for other animal species, including beetles, collembollans and mites.



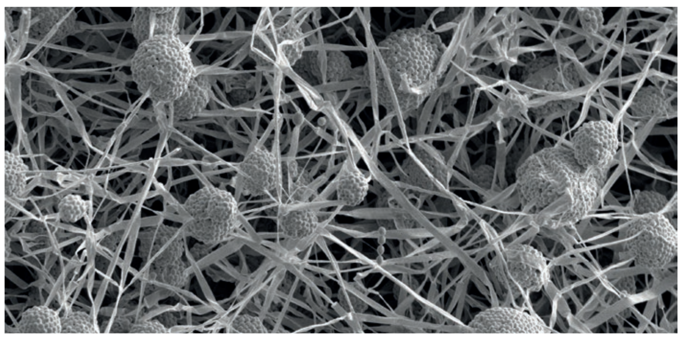
Global distribution of deserts. The map was created from the World Wildlife Fund's (WWF) Global Ecoregions database. Deserts cover more than one fifth of the Earth's land surface and are found on every continent. The largest hot desert in the world, North Africa's Sahara, reaches temperatures of up to 50 °C (derived from Olson *et al.*, BioScience, 2001). (LJ, JRC) [12]

Anthropogenic ecosystems – Agroecosystem

Productive, managed and transformed

Agroecosystems are natural ecosystems that have been modified by humans to produce food, feed, fibre and fuel. Defined by a combination of plant-growing period (in days), climate and soil types, agroecosystems are extensive and diverse. They make up more than 40 % of the Earth's land area: 1.8 and 3.6 thousand million ha for crops and livestock, respectively, and encompass the ancient and fragile soils of Australia and Africa to the relatively young and fertile soils of Europe, Asia and North America. While they coexist with natural terrestrial ecosystems, agroecosystems have been modified extensively since the inception of agriculture 10 000 years ago. They support non-indigenous, domesticated plant species, including crops such as grains (e.g. wheat, maize and rice), legumes (e.g. peas and beans), oilseeds (e.g. canola, soybean and cotton) and pastures (e.g. ryegrass and clover).

Agroecosystem soils have been modified through intensive management practices, such as cultivation, grazing, plant product and residue removal, the addition of fertilisers and pesticides, irrigation, flooding and the creation of drainage systems. Some have been transformed to such an extent that they require reclassification or are deemed 'new soils', and classified as Anthrosols. Over the past 60 years, global increases in crop and livestock production systems have also coincided with substantial erosion problems, loss of carbon and nitrogen, salinisation, acidification and increased pest incursions, to the point that the conservation of soil resources and soil quality is a critical priority globally. Several countries are addressing soil decline issues both through voluntary and regulated soil-conservation strategies, such as satellite-guided controlled field traffic systems, direct drilling, integrated pest management, targetted fertilizer application, diversified crops, cover cropping, plant-residue retention, rotational grazing, liming and subsoil manuring. The extent and diversity of modifications to soil agroecosystems has given rise to both a diverse and dynamic range of biological habitats and, in turn, to diverse and dynamic biological soil communities.



A mass of fungal hyphae with spore heads in a cultivated soil. (PM)

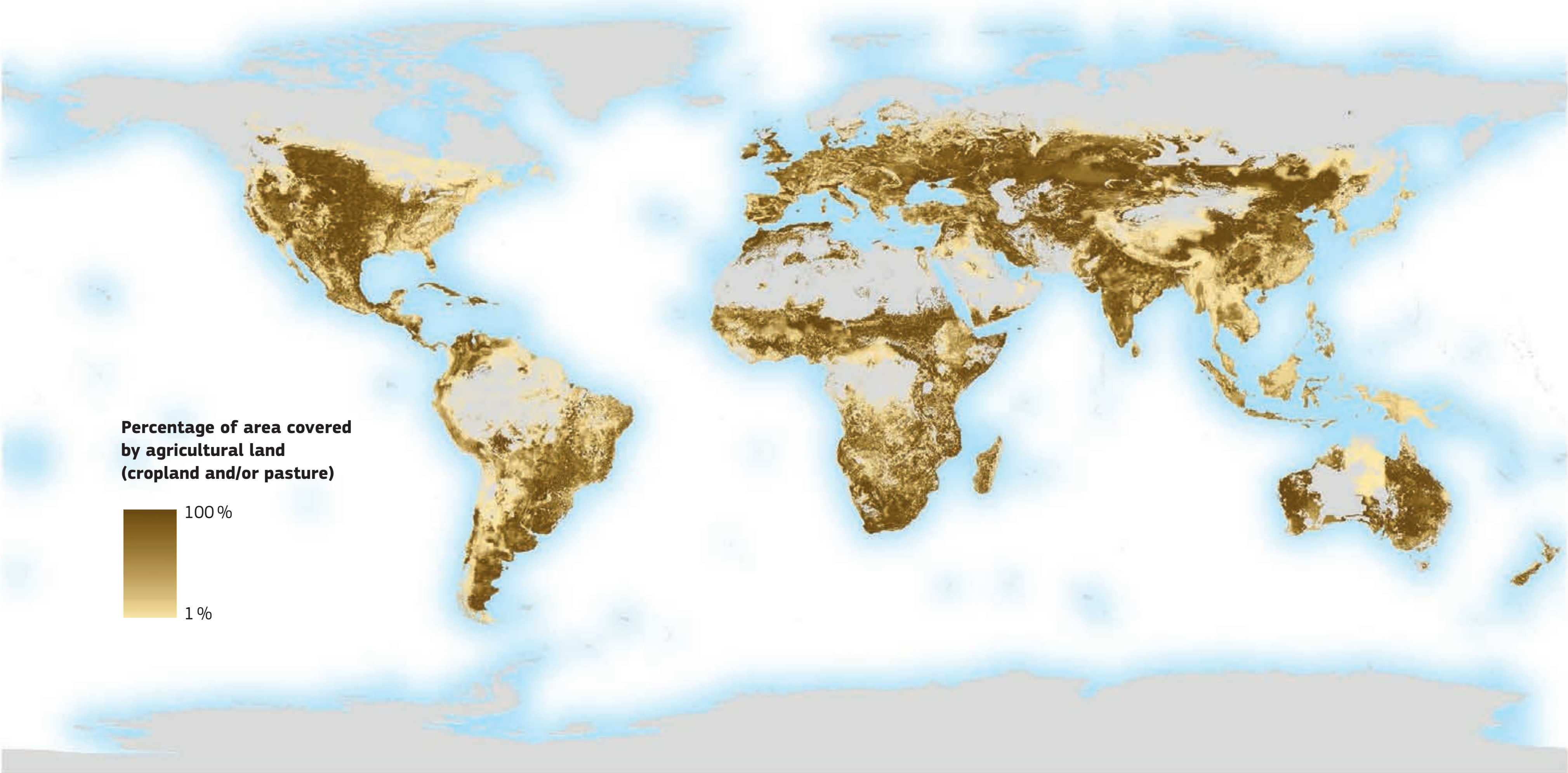
Agroecosystems include not only (**a**) lands used to grow and harvest crops (i.e. croplands), but also permanent crops, such as (**b**) pastures and (**c**) orchards. (MIM)

Soil biodiversity

The soils of the world's agroecosystems contain biota that are visible to the naked eye (e.g. earthworms, dung beetles, ants and termites – see Chapter II) as well as those that can only be seen with the aid of a microscope. These range from micro- and mesofauna (e.g. mites and collembolans – see pages 49-50) to microorganisms and microfauna (e.g. bacteria, fungi, archaea, protists and nematodes – see Chapter II). The application of genetic tools, involving the direct extraction of soil DNA and RNA (see pages 64-65), has allowed researchers to measure the most abundant, as well as the rarest, biota, particularly those at the microscopic level. [112]

Generalisations can be made about the relative influence of various factors in shaping bacterial communities at the phylum level based on a number of surveys in the USA, Europe (mainly France, the UK and the Netherlands), China and Australia. The common taxa or groups that make up agroecosystem biodiversity are now well described. Bacteria are by far the most diverse of the soil biota, with more than 30 groups (phylum levels) routinely identified in even the most disturbed agroecosystems, such as in hydrocarbon-contaminated sites and rice-paddy soils. The 'agriculturally significant' functions associated with the modification of soil structure, the mixing of organic material, the mineralisation of nutrients, the promotion of plant growth, the control of pathogens and the remediation of herbicides attributable to these taxa are also becoming more easily identified.

Research assisted by DNA and informatic technologies is enabling the identification of characteristic soil biological communities for many land uses, which is providing baseline data for long-term global monitoring programmes. All features of the habitats that make up global agroecosystems, including the chemistry, structure, input and disturbance regimes, plant diversity and growth cycles, provide the critical metadata needed to describe the current and future status of soil biodiversity. It enables both the reconstruction of soil biodiversity patterns from pre-agricultural times and the prediction of long-term impacts of agricultural management regimes. These approaches will improve restoration efforts and provide decision support to land managers who wish to manage their soils sustainably (see Chapter VI) into the future.

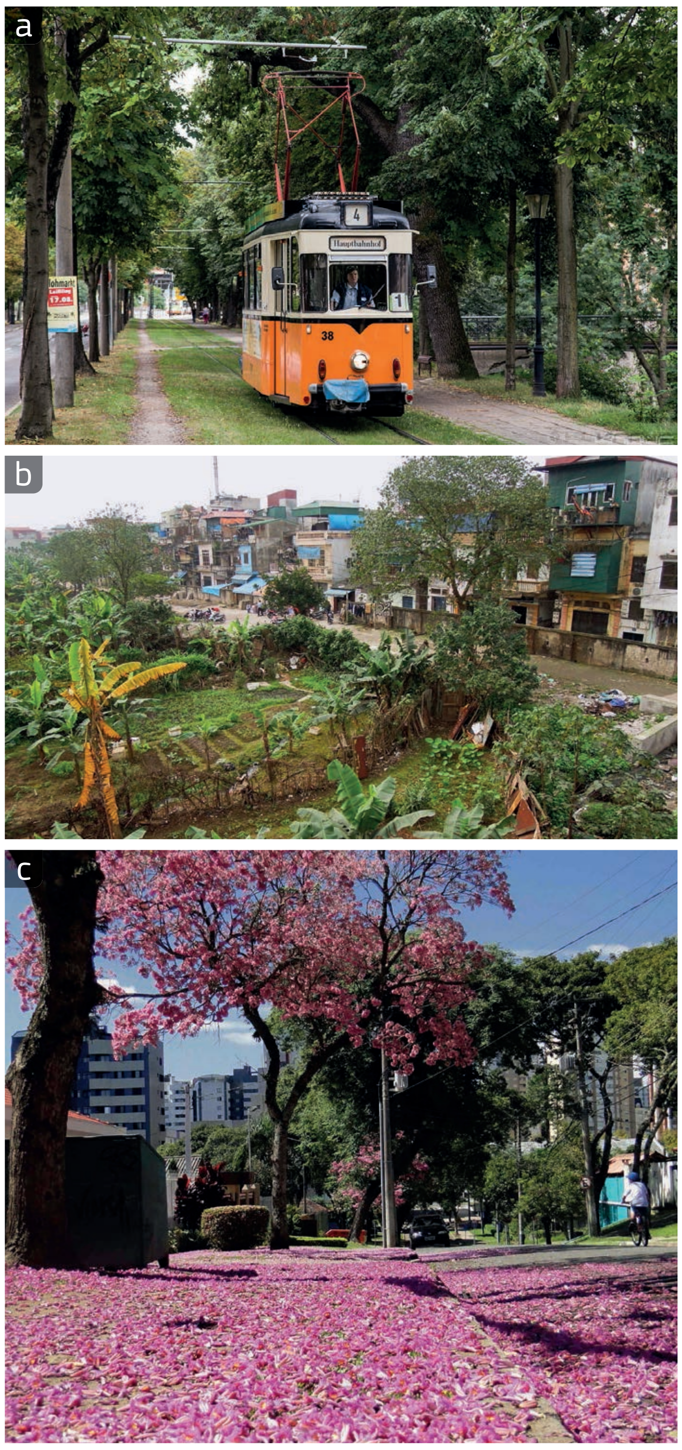


Global distribution of agricultural areas. The map shows both cropland and pasture areas in 2000, including the percentage of area covered by agricultural land (derived from Ramankutty *et al.*, Global Biogeochemical Cycles, 2008). (LJ, JRC) [113]

Anthropogenic ecosystems – Urban ecosystem

Built, populated and growing

There is no general agreement on a definition of what is urban, and considerable differences in the classification of urban areas exist among countries and continents. In Europe and North America, the urban landscape is often defined as an area with human agglomerations and with a built-up surface of > 50 %, surrounded by other 30 - 50 % built-up areas, and overall a population density of more than ten individuals per hectare. In other contexts, population size, the density of economic activity or the form of governance structure are used to delineate towns, cities or city regions, but there is significant variation in the criteria for defining what is urban. While everyone struggles to define exactly what is meant by a city, nobody negates the shifting patterns of urbanisation or the overall growth of cities.



Urban soils in (**a**) Germany, (**b**) Vietnam and (**c**) Brazil show the very different potential habitats for soil organisms in a city. (KU, DMK, AJJ)

Soil biodiversity

Urban soils are subjected to many pressures. Sealing and compaction by vehicles and humans reduce the soil's permeability to water and air. Furthermore, urban soils tend to accumulate pollutants, mainly heavy metals, from industrial and transport emissions (see pages 120-121). A study showed that soils in cities are generally 1 - 2 °C warmer, 50 % drier and 1.5 times more dense and lower in organic carbon than similar soil types in the rural environment. All of these aspects affect abundance, diversity and processes carried out by belowground urban life. The interest in understanding urban ecosystems is recent and is leading to an increasing number of studies that describe the soil organisms of green spaces within large cities. For example, soil macrofauna was investigated in urban parks and domestic gardens in London, UK. Five groups of organisms were identified: earthworms, ants, isopods, millipedes and centipedes (see Chapter II). The species densities of the studied soil organisms were comparable to those found in natural ecosystems. [114]

Carabid beetles (see page 59) were collected in a metropolitan area in South Korea. Carabid assemblages changed significantly in response to management practices (i.e. mowing). Isopod assemblages were studied in Budapest, Hungary. The data analyses revealed high species richness compared to the total number of species in the country. This may be due to the ecological process known as homogenisation. Biotic homogenisation entails the replacement of native species with non-natives, a process that plays an important role in shaping urban fauna and flora by increasing the similarity of soil communities among cities worldwide. This phenomenon has been observed not only in isopods but also earthworms and millipedes. Another aspect that is increasingly studied is the impact of urbanisation on soil organisms. For example, nematode (see pages 46-47) assemblages were studied along an urban-rural gradient of land use in the USA. Results showed that there were functional differences in the nematode communities along the land-use gradient, thus confirming that the functional composition of the soil food web is an important component of soil biodiversity that can be affected by urbanisation.

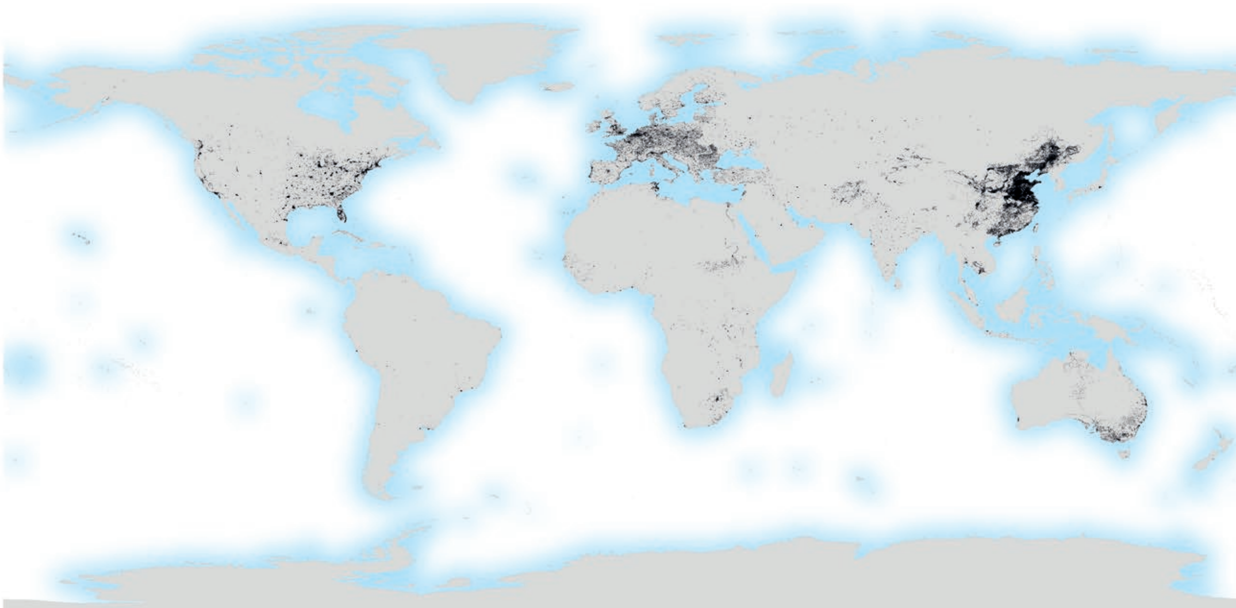
Soil biodiversity in Central Park

- Central Park is a recreational area in Manhattan, New York City, USA. It was initially opened in 1857 and is one of the most frequently visited urban parks in the world.
- Aboveground, Central Park harbours approximately 393 plant species, more than 250 species of vertebrates and more than 100 species of invertebrates.
- In 2014, researchers collected 600 soil samples in order to investigate the diversity of soil archaea, bacteria, fungi, protists, invertebrates and other eukaryotes. [115]
- The soils of Central Park harbour nearly as many distinct soil microorganisms as are found in biomes across the globe.
- Despite high variability across the park, belowground diversity patterns were predictable based on soil parameters, in particular soil pH.
- The study demonstrates that even an urban, managed system contains large amounts of undescribed soil biodiversity.

Bird's-eye view of Central Park in New York City (USA). It covers an area of about 3.5 km² (0.80 km by 4.02 km) and hosts an incredible soil biodiversity. (AQU)

Uniqueness of urban soils

The ecological uniqueness of cities and their continuous growth due to the increasing population size, probably means that the soils of urban areas should be considered as a particular habitat. Several factors make urban soils unique: conditions that promote the spread of invasive species (see page 119), the strong influence of human activities prior to urbanisation (e.g. industrial and waste disposal), and the creation of novel soil types with anthropogenic materials (e.g. cement). Furthermore, urban environments may feature a complex mosaic of habitats for soil organisms, from urban parks and private gardens and lawns to roundabouts and sports and leisure areas. Soil biota have been shown to respond to alterations in soil properties associated with urban environments. The effect of these urban pressures on belowground biodiversity is an alteration of ecosystem functions and processes. Nevertheless, the diversity of urban soils may also represent hot spots for soil biodiversity. For example, soil microbial communities in Central Park in New York City are comparable to those found in natural ecosystems (see box above).



Global distribution of artificial areas. All urban and related features are included in this map, for example urban parks and industrial areas. The map was created with data from the FAO's Global Land Cover Share Database. (LJ, JRC) [13]

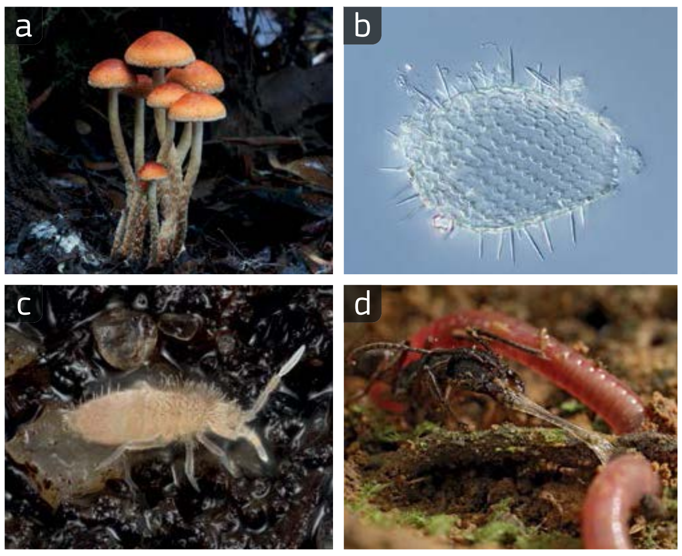
Map of global distribution of soil biodiversity

Mapping soil biodiversity

While scientific knowledge of individual groups of soil fauna, together with their role in providing key ecosystem services, is continuously evolving, data on their abundance, diversity and geographic distribution remain scarce. Although the major ecosystems of the planet are now relatively easily mapped and monitored through the vast quantities of data collected by various satellite-based sensing systems, such tools are unable to provide any direct information relating to soil-based organisms. In fact, any comprehensive or large-scale survey and monitoring programme for soil organisms can only be carried out through direct field observations or sampling. Therefore, knowledge of belowground species distribution is very incomplete and, as a consequence, there is a general lack of maps showing the degree of soil biodiversity, especially at global scales.

In addition to the practical problems associated with mapping soil biodiversity, the issue is further compounded by the lack of a precise definition (e.g. does biodiversity relate to total number of species present, the genetic diversity within species, the distribution of individuals among those species, etc.?). When combined with the practical challenges associated with collecting data, the task becomes even more daunting!

It is interesting to note that recent studies have found that the aboveground biodiversity of a region (i.e. the number of species of vascular plants, amphibians, reptiles, birds and mammals) are strongly correlated, at least on a global scale, to the number of soil types in the same area (a concept referred to as pedodiversity). Additionally, findings show that pedodiversity can in turn be used as a broad indicator of aboveground biodiversity, which itself can often be difficult to quantify. Moreover, there is increasing recognition of the influence of these components on each other and of the critical role played by above- and belowground feedbacks in controlling key ecosystem processes.



Soil biodiversity is extremely diverse, from (**a**) fungi and (**b**) protists to (**c**) collembolans and (**d**) ants and earthworms, and mapping it at global scale is difficult. (SA, EDM, WVE, SSH)

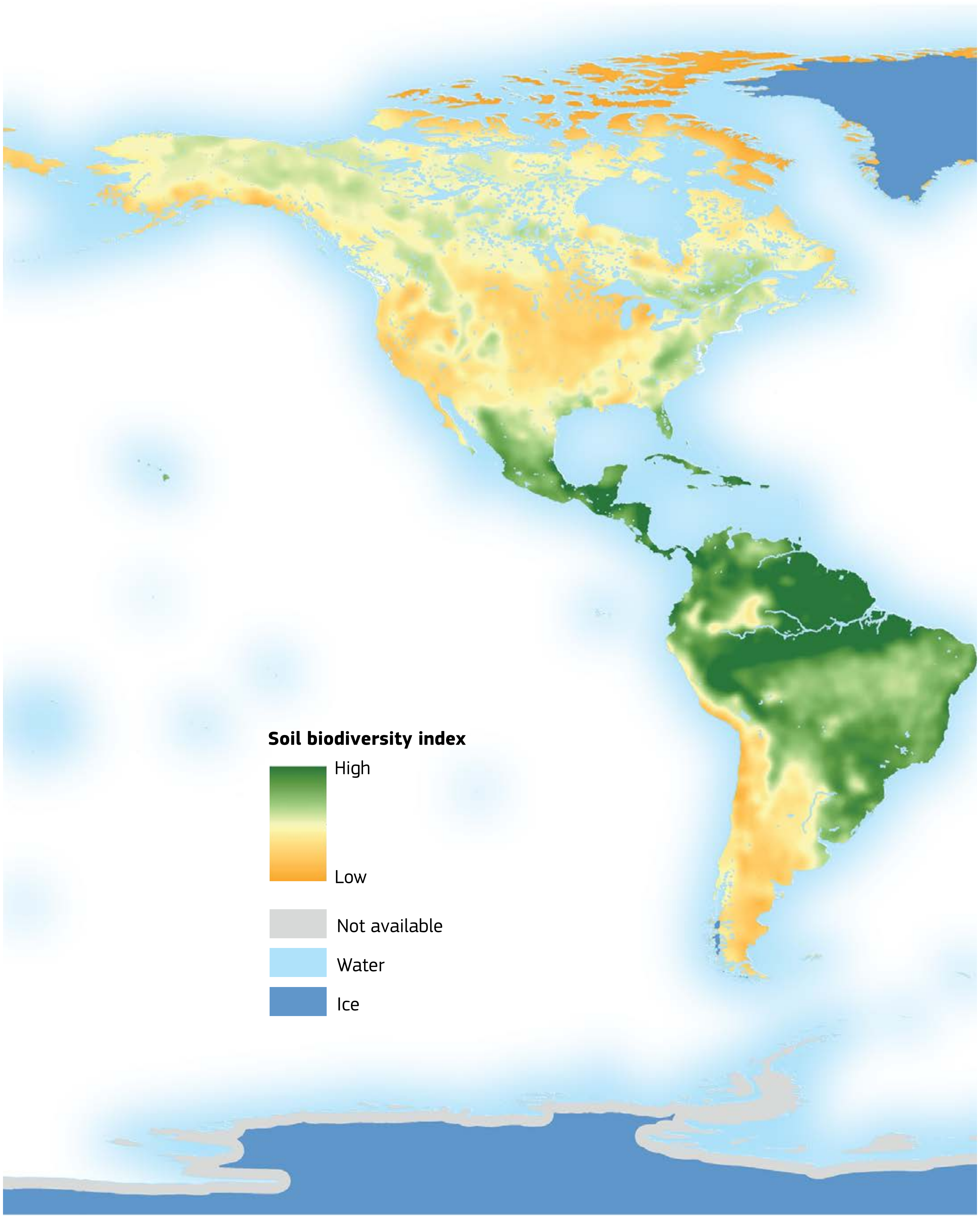
Methodology

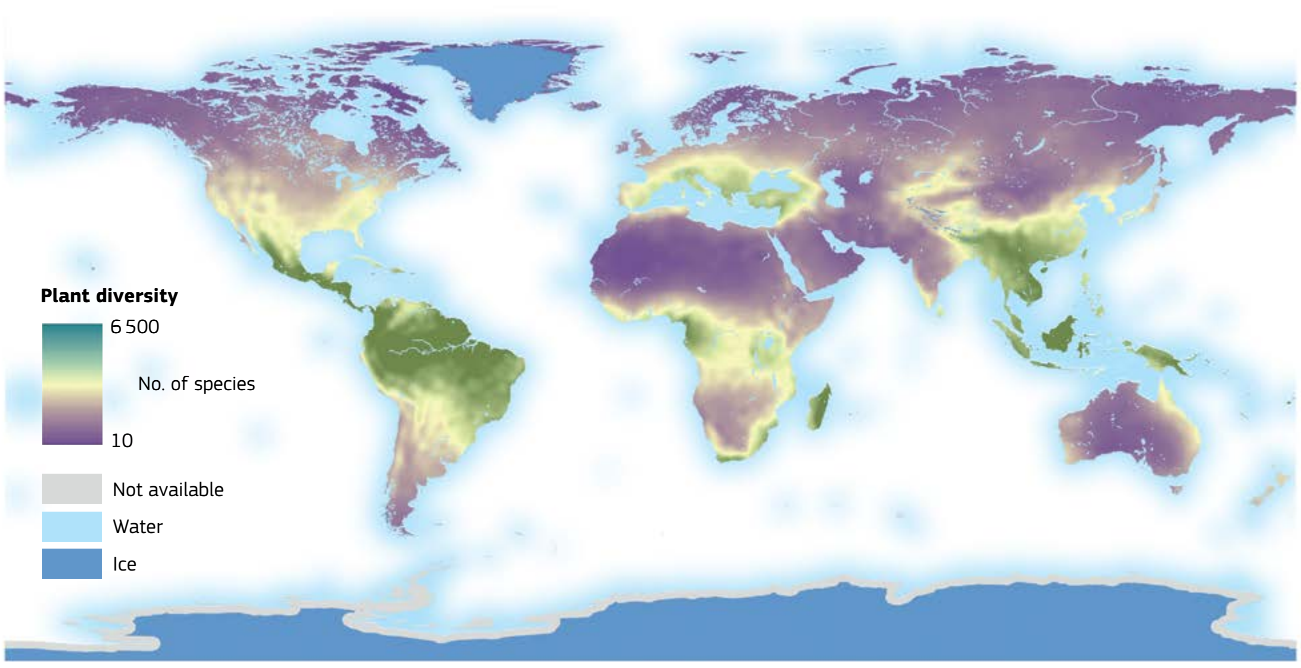
As seen in this chapter, there are numerous groups of soil organisms distributed in different ways across the globe. Also, there is a significant lack of data for many groups of soil-dwelling organisms at global scale. Furthermore, as numerous factors influence the geographical patterns of soil biodiversity, it is not easy to give a static representation of soil biota distribution on a map. For all these reasons, it is difficult to obtain a reliable global map showing the distribution of all soil biodiversity.

Nevertheless, the available data can be used to develop a simple index describing the potential level of diversity living in soils on our planet. In order to make this preliminary assessment, two sets of data were used:

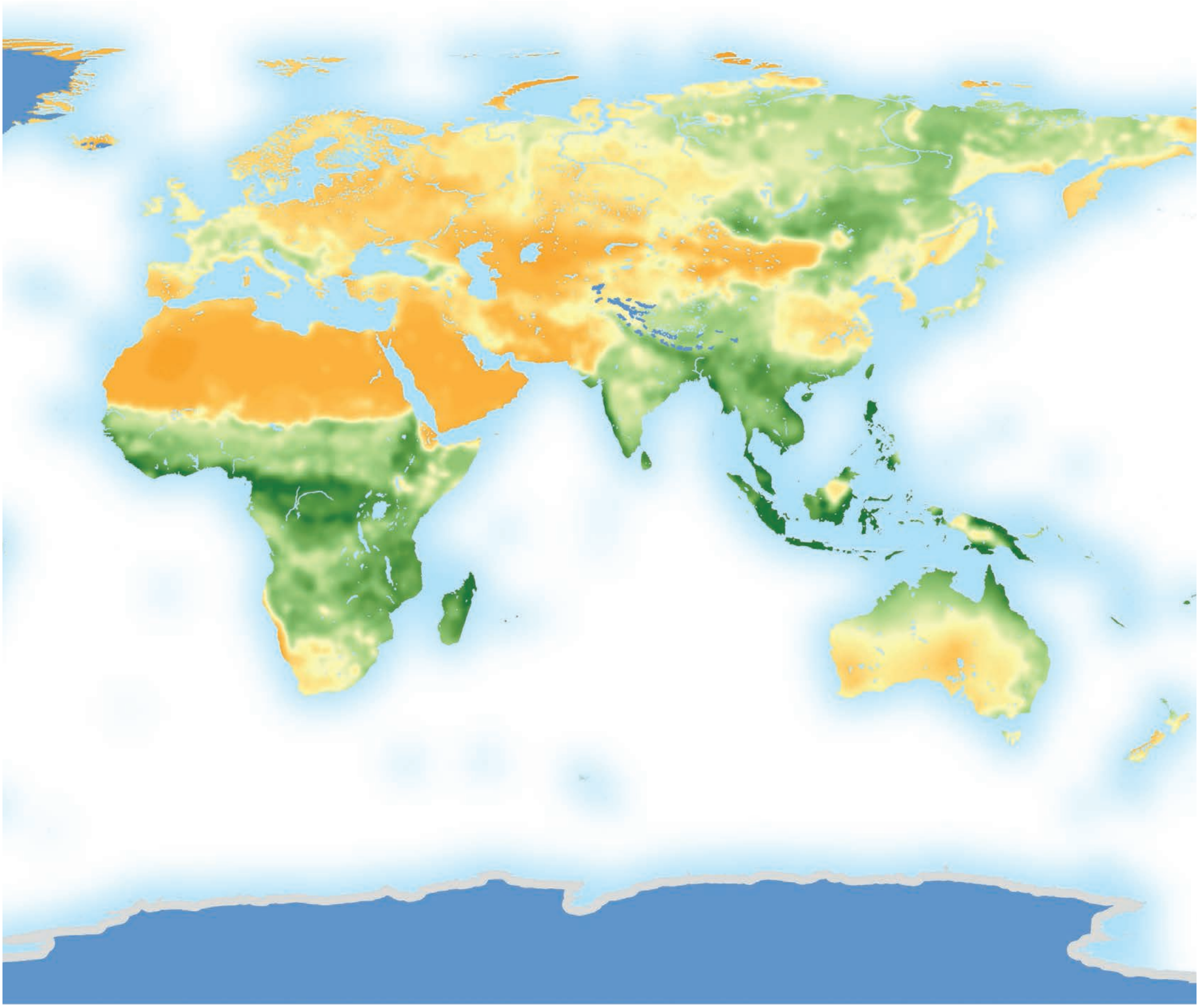
- distribution of microbial soil carbon developed by Serna-Chavez and colleagues (see page 69). This dataset was used as a proxy for soil microbial diversity
- distribution of the main groups of soil macrofauna developed by Mathieu (see page 71). This dataset was used as a proxy for soil fauna diversity

The two datasets were then harmonised on a 0-1 scale and summed. The total scores were categorised into an index ranging from low (i.e. poor level of soil biodiversity richness) to high (i.e. significant level of soil biodiversity richness).





In comparison with the soil biodiversity index map, the plant diversity map shows that areas near the Equator that receive high precipitation and have constantly high temperatures have the highest plant biodiversity. Outside those areas, the highest biodiversity is found in Mediterranean climates where temperatures are moderated by the vicinity to the ocean, seasonal precipitation and varied topography which create micro-ecoregions (derived from Kreft and Jetz, PNAS, 2007). [116]



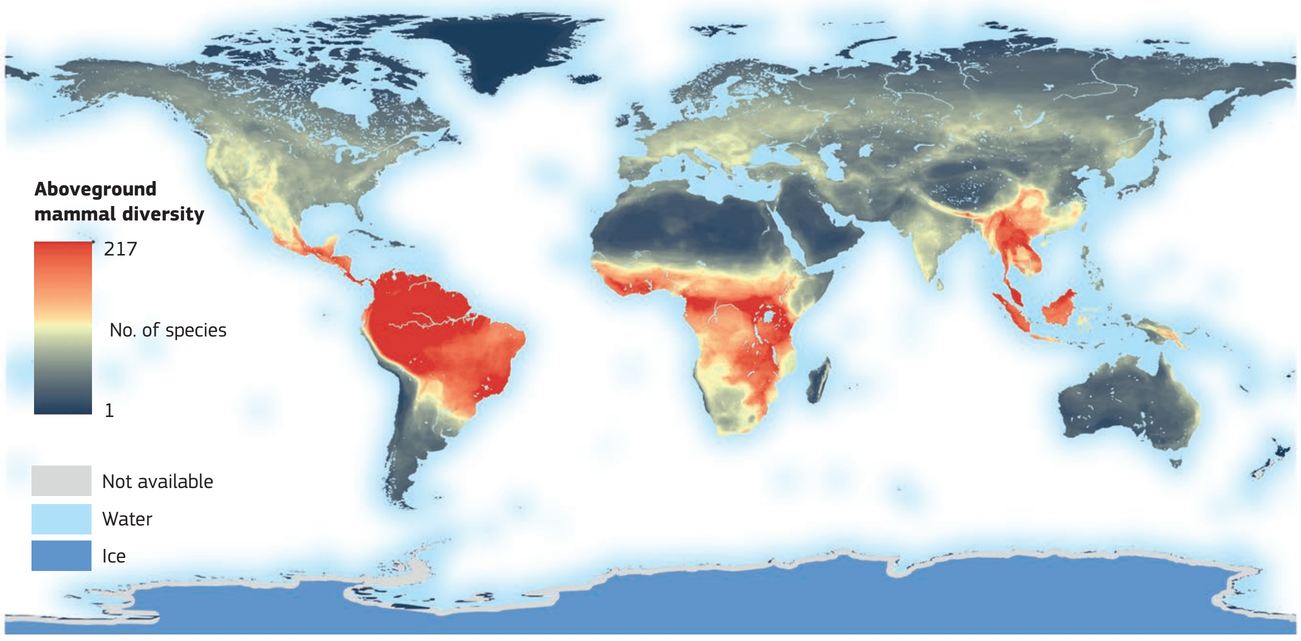
Results

The resulting map is an initial attempt to denote global soil biodiversity levels. The pattern reflects the discussion on the previous pages, which describes the soil biodiversity associated with various biomes.

The analysis shows that most soil biodiversity is found in both humid-temperate and humid-tropical soils, followed by soils where extremes in temperature and precipitation levels are generally absent. Lower levels are found in cooler and drier soils (such as boreal and Mediterranean climates). The lowest soil biodiversity levels are associated with the presence of extreme heat or very cold soils.

It is important to note that this is a simplistic exercise based on two datasets showing the distribution of only a few groups of soil organisms (see pages 69, 71). Further refinement could be provided by including soil microfauna (e.g. nematodes) and mesofauna (e.g. collembolans and mites).

While designed to stimulate debate, this map also gives a clear message of the need for significantly more research and data collection.



By contrast, the map of diversity of aboveground mammals indicates the concentrations of mammal species across the planet (areas of deep red and yellow indicate the greatest diversity of species, while shades of blue indicate areas of lower biodiversity). As for plants, higher levels of biodiversity are found in the tropics closely followed by temperate regions (derived from Pimm *et al.*, Science, 2014). [117]

Soil biodiversity underpins several functions that allow for the correct functioning of ecosystems. These functions generate benefits, known as ecosystem services, for human beings, including the provision of food and clean water, climate regulation, support of human habitats and contribution to cultural values. (GS/CIAT, NP/CIAT, DNO, GKN, MFE, NASA)

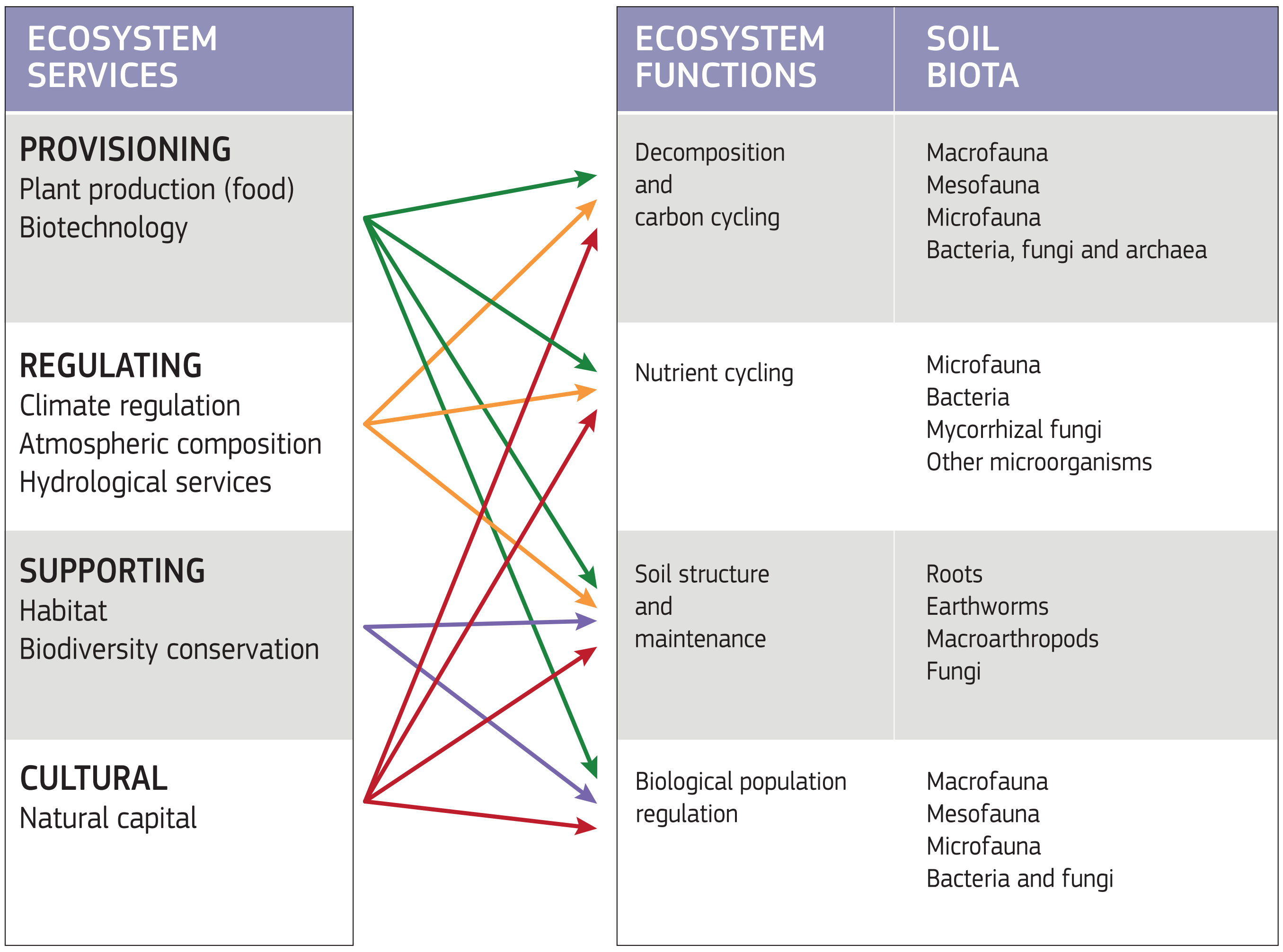
Introduction

Soils start to exist when organisms organise their habitat. They build and maintain soil structure and influence its chemical properties by weathering bedrock, aggregating mineral and organic constituents and developing the pore network. This affects the movement of water and gases, the transfer of nutrients and energy, and the removal of metabolic products, which contributes to the many functions and ecosystem services soils provide. [118]

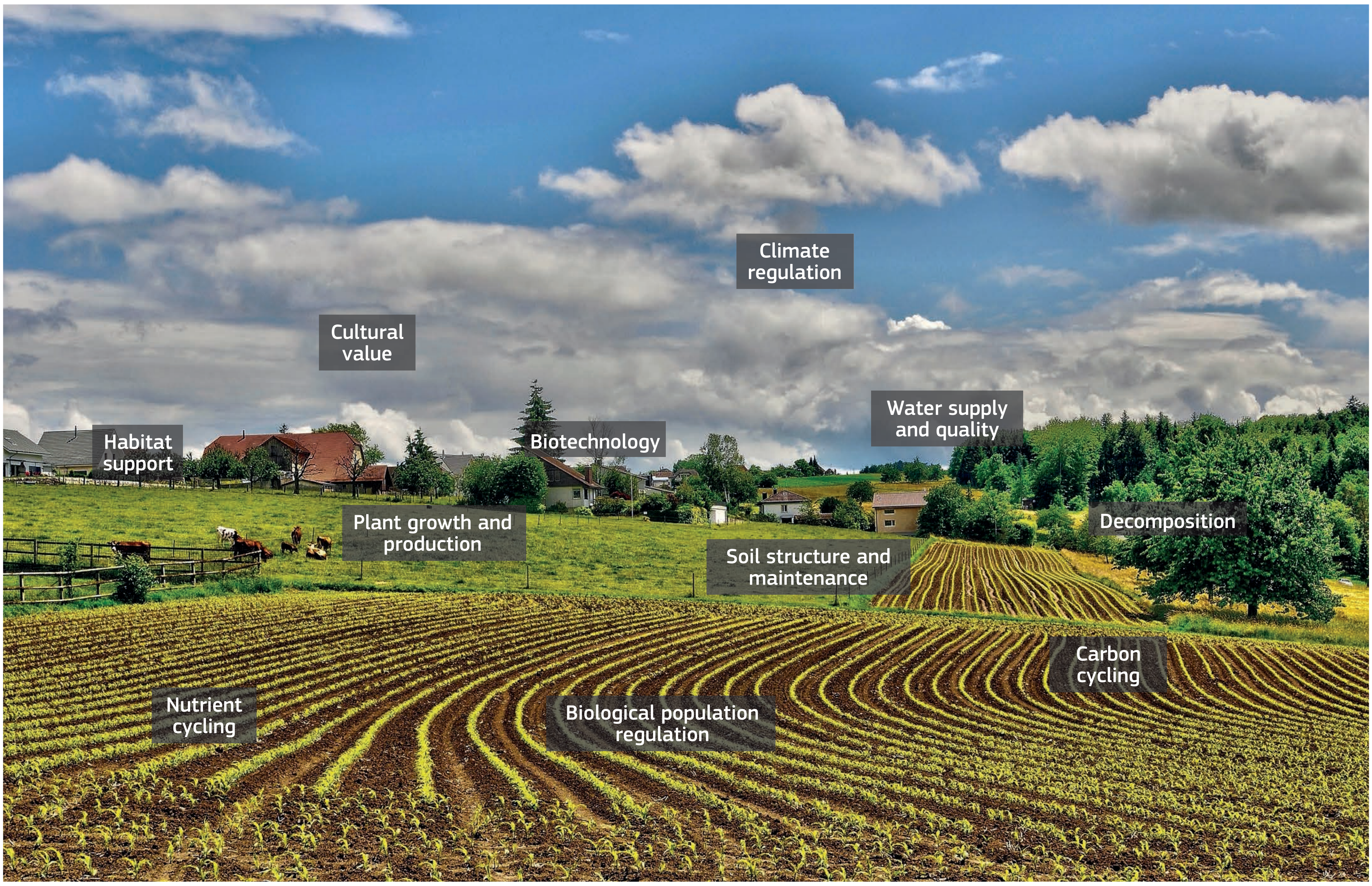
The terms ecosystem 'functions' and 'services' are often confused. 'Functions' is used to define the biological, geochemical and physical processes and components that take place within an ecosystem. 'Services' is used to encompass the tangible and intangible benefits that humans obtain from ecosystems. Considering soil, it is possible to say that ecosystem services are derived from different soil system functions and, in turn, each ecosystem service is associated with specific groups of soil biota.

The Millennium Ecosystem Assessment, compiled by the United Nations in 2005, represents a major overview of the effects of human activity on the environment. According to this document, there are four recognised classes of ecosystem services: 1) Provisioning; 2) Regulating; 3) Supporting; and 4) Cultural. Provisioning services pertain to products, such as food and fresh water. Regulating services include benefits, such as climate control and disease and pest control. Supporting services include soil formation and habitat sustenance that are necessary for the maintenance of all soil functions, and provide a suitable rooting medium for plants. Cultural services are the non-material benefits that people obtain from ecosystems, such as cultural heritage, recreation and tourism.

Soil and its biota provide these ecosystem services by contributing to the provision of food, fuel and fibre, the infiltration, storage and delivery of clean water, the suppression of plant pests, the control of nutrient cycles, and the provision of cultural value. This chapter presents and discusses these functions and services provided by soil-dwelling organisms.



Soil-based ecosystem services, ecosystem functions and soil organisms that support them. The terms 'functions' and 'services' can be confusing. Usually, functions are considered as the biological processes underpinning and maintaining the ecosystem, while ecosystem services are defined as the direct and indirect contributions of an ecosystem to human well-being (derived from Brussaard, 2012). [119]



The contribution of soil and its biota to the provision of ecosystem services in a mixed landscape. Ecosystem services are the benefits people obtain from ecosystems. These include provisioning services, such as food and water; regulating services, such as pest and disease control; supporting services, such as habitat provision, that maintain the conditions for life on Earth; cultural services, such as the educational value of ecosystems. (JDE)

Introduction

Factors affecting ecosystem functions and services

In soils, ecosystem functions and services result from the interaction of physical, chemical, biological and human factors. These processes operate at different scales of time and space, integrated into each other, and are organised hierarchically. Climate, which operates at the largest scales of time and space, is always the most important factor influencing the provision of ecosystem functions and services. This is followed by the quality of the substrate (i.e. nutrient availability, determined by the initial mineralogy of the parent material), plant communities and the quality of organic matter that they return to the soil. At the smallest scales, the key factor is biodiversity, ranging from invertebrates to microbial communities (see Chapter II). [2]

	TEMPORAL AND SPATIAL SCALE
CLIMATE	1 000's of years, km^2
↓↑ CLAY + NUTRIENTS	100's of years, ha
↓↑ VEGETATION AND RESOURCE QUALITY	years, $10\,m^2$
↓↑ MACROORGANISMS MICROORGANISMS	days, mm^3
Biological interaction ↓	
SOIL FUNCTIONS AND SERVICES	

Hierarchical organisation of the physical, chemical and biological factors of soil functions and services, and the ranges of temporal and spatial scales at which they operate. (PL)

Physical factors

Physical properties comprise all climatic factors, such as temperature, moisture and their daily and seasonal fluctuations; they determine the rates of metabolic processes in the soil and interact with the physical properties of soil. For example, the total amount of water that can be retained in soils, and the energy used to attach that water to soil particles, depends on the amount and size of the soil pores. This physical property of soil is known as porosity. There are two different types of pores: textural pores, which occur between soil particles, and structural pores, which are created by physical processes and biological activities.

Mysterious mound-field landscapes

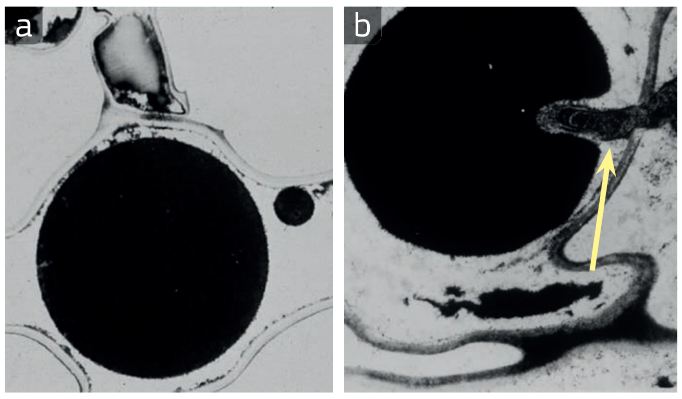
- Seasonally flooded savannahs in French Guiana are dotted with thousands of regularly spaced small, round earth mounds
- Although these look like the result of ants and termites activities, they were in fact originally built by pre-Columbian farmers to grow crops. [120]
- Raised fields were abandoned by farmers around 800 - 400 years ago. But surprisingly, remnants continue to be visible today.
- After abandonment, and probably even before, raised fields attracted a diverse community of flooding-intolerant organisms, such as ants, termites and earthworms.
- The physical properties of soil mounds are caused by biological factors: compact aggregates produced by social insects and earthworms enhance the soil stability, and the dense network of galleries enhances water infiltration.
- Mounds have been maintained for centuries. In accomplishing this, soil organisms maintain only the habitat that has limited risk of flooding and ensure their own survival all year-round.

Remnants of pre-Columbian raised fields in seasonally flooded savannahs in French Guiana. (**a**) Aerial image of a raised-field landscape shaped originally by human ecosystem engineers. (**b**) Ground-level image of ancient raised fields that are maintained above the wet-season water level through the ecosystem engineering activities of ants, termites and earthworms. (DRE, DMC)

The aggregation of soil particles is another physical process that influences the provision of ecosystem services. It involves the organisation of the mineral and organic elements of soil (see Chapter I) into structures of different sizes, called soil aggregates (see page 72). Similar to pores, aggregates can be derived from physical or biological processes. Physical aggregates formed by alternation of wet and dry or freeze and thaw periods have sharp edges and usually do not allow large amounts of interaggregate pores to form. These aggregates are mostly stabilised by purely physical forces (such as Van der Vaal's forces between particles). However, living organisms often play a key role in creating these aggregates (known as biogenic aggregates) by producing the 'glues' (for example, the protein glomalin produced by arbuscular mycorrhizal fungi – see page 40) that stick particles together. Biogenic aggregates may be formed by natural physical forces, such as those of growing roots, or physically generated, such as nests and other constructions made by social insects (termites and ants – see pages 54-55) and the organo-mineral casts of earthworms (see page 58).

Chemical factors

Chemical processes include all the transformations that organic residues undergo during the decomposition process (see page 106). Plants produce residues of different qualities. For example, the presence of polyphenol compounds accumulated in plant leaves limits herbivory and greatly reduces decomposition rates: in dead leaves, more than 80 % of nitrogen is locked up in phenol protein complexes that only a few microorganisms, such as the white-rot basidiomycete fungi (see pages 38-39), can decompose. Decomposition processes recycle nutrients, making them available again to plants of storing them as resistant compounds that play an important role in soil functions and services, including nutrient cycling and climate regulation.



Polyphenol protein complexes (in black) block > 80 % of available nitrogen in leaf litter in chemical forms that are only degraded by white-rot fungi (yellow arrow indicates a fungal hypha). (GVI)

Biological factors

Biological processes involve both microbial and faunal functions, which inevitably interact with other soil components. In fact, microbes are the ultimate operators of all chemical transformations in the soil: they facilitate nutrient release through decomposition processes, conservation of organic matter through synthesis of resistant humic compounds, and nitrogen fixation. They also help, to some extent, aggregate of mineral and organic particles into solid structures by producing polysaccharides, which glue particles together, or entangling particles into 'nets' of fungal filaments. Invertebrates (including micro-, meso- and macrofauna – see page 31) play a unique role in mechanical activities by softening, fragmenting and burying plant residues, which facilitates their natural decomposition, and creating channels and pores in the soil that provide habitats for smaller organisms and reservoirs and routes for air and water to circulate and be stored. In addition, invertebrates produce compounds that stimulate plant growth and protection against pests and diseases (see pages 108-109).

Different species of soil organisms create structures that form their respective functional domains: biogenic aggregates produced by (**a**-**b**) termites, (**c**) cicadas and (**d**) earthworms. (ABR, IPA, PL, RB)

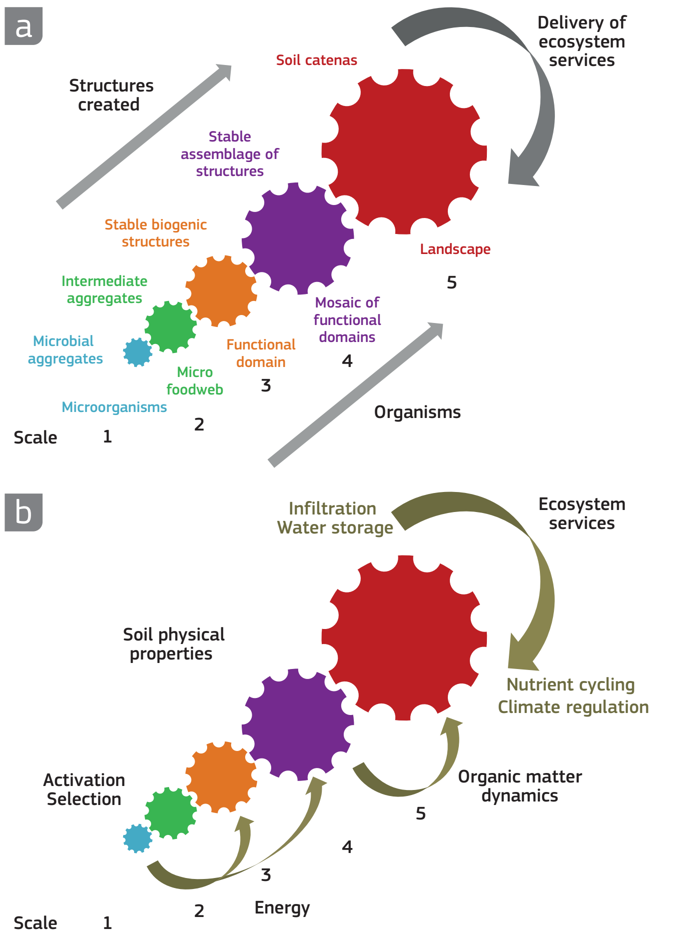
Human activities, such as intensive agricultural practices (e.g. tillage, pest control and chemical fertilisation), can indirectly affect soil functions by altering the composition and structure of the soil communities. (NP/CIAT)

Human factors

In addition to natural factors, another force is becoming prominent in shaping ecosystem functions and services. Human activities modify soil systems, mostly by manipulating plant communities in managed productive systems, altering the soil structure through tillage and indirectly affecting soil biodiversity by reducing abundance and diversity through the excess use of pesticides and/or mineral fertilisers (see pages 122-123).

Spatial scales of soil biodiversity functions

Soil functions are a consequence of the complex interactions between different groups of microorganisms, as well as between micro-, meso- and macrofauna. Therefore, a reductionist approach, which involves separating the effects of single species, is of limited help in understanding soil biodiversity functions. We must adopt an integrated approach that takes into consideration interactions between organisms, the physical structures built in the soil that they inhabit and the spatial and temporal scales at which these entities operate. Soil organisms have coevolved for hundreds of millions of years and interact in positive (mutualistic – see box on page 33) and negative (e.g. predator versus prey – see box on page 96) ways. In the soil environment, movements are limited by its compact structure; feeding is often difficult due to the generally low quality of resources available, and metabolism rates have to adapt to the alternation of dry and moist periods. No organism is able to face all of these challenges alone. Soil microbes are generally reliant on the action of ecosystem engineers, namely roots (see page 43) and invertebrates (e.g. earthworms – see page 58), along with percolating water, to obtain food. Invertebrates in turn, use the decomposition capacities of microorganisms in different types of mutualist associations to obtain their nutrition from soil. From the smallest (soil pores and aggregates – see page 72) to the largest scales (ecosystems and landscapes), numerous organisms interact to establish a limited number of associations that drive and regulate ecosystem functions and sustain ecosystem services. At each of the five recognised scales, soil organisms form distinct assemblages that live in specific niches, interact and carry out explicit functions. [121]



(**a**) Self organisation of microorganisms (blue), microfauna (micro food web – green), plant roots and invertebrates (ecosystem engineers – orange) at different scales in soils. (**b**) Contribution of the different groups of soil organisms to the establishment of structures and delivery of ecosystem services. Ecosystem engineers activate and select microorganisms that decompose organic matter; the derived energy is then used by the ecosystem engineers to produce physical structures (e.g. tunnels) that influence water infiltration and storage. Furthermore, the organic matter dynamics and soil physical structure allow for carbon sequestration in both soil and plant tissues, thus contributing to nutrient cycling and climate regulation. (PL)

Scale 1

At Scale 1 (a few micrometres), microbial communities (i.e. archaea, bacteria and fungi – see Chapter II) form colonies living in pores inside aggregates or in the inter-aggregate space. They may create small structures using slime (polysaccharides) known as microbial aggregates. Once they have utilised all the organic substrates or nutrients available, they either die, or can enter into dormant stages (see box on page 34) since they generally have very limited abilities to move to new substrates. Fungi can extend their mycelium over large distances, although the distribution of their spores is largely performed by invertebrates and roots.

Soil ecosystem engineers have the ability to build resistant structures (tunnels and nests) and create pores by moving through and mixing soil. They include (**a**) ants and (**b**) plant roots. (CWA, AES)

Chemical versus ecosystem engineers

- Depending on the main functions carried out, soil organisms can be assigned to one of the following two main functional groups:
  - chemical engineers (transformers and decomposers), i.e. organisms responsible for carbon transformation through the decomposition of plant residues and other organic matter, and for the recycling of nutrients (e.g. nitrogen, phosphorus and sulphur);
  - ecosystem engineers, i.e. organisms responsible for maintaining the soil structure through the formation of pore networks, bio-structures (e.g. earthworm casts) and aggregation, or particle transport.
- Microorganisms, such as bacteria and fungi, are by far the most important chemical engineers; over 90 % of the energy flow in the soil system is mediated by microbes.
- Earthworms, termites, ants and plant roots are the most important ecosystem engineers. However, soil engineers also include many other invertebrates, such as millipedes, centipedes, beetles and scorpions, which may be more or less responsible for soil formation.

Termites are included in the functional group of ecosystem engineers (USDA)

A fungus surrounding the root of a maize plant. One of the main functions of soil microorganisms, such as fungi, is to decompose organic matter and make minerals available to plants. (WVE)

Scale 2

Scale 2 refers to the soil micro food webs, a complex community of small invertebrates (e.g. nematodes, mites and collembolans – see pages 46-47, 49-50) that usually feed on microorganisms, thereby regulating their community abundance and composition.

Scale 3

Scale 3 is that of the ecosystem engineers (see box on page 95). At scales of centimetres to metres or more, they mix the soil and can build sophisticated networks of connected pores and channels and may produce huge amounts of biogenic aggregates (e.g. earthworm casts). These structures play a vital role in soil functioning, and can have large effects on the flow of water and nutrients within the soil system.

Earthworm casts influence ecosystem functioning. They are hotspots for microorganisms and, when desiccated, show increased stability compared to the surrounding soil. (RMR)

Scale 4

Scale 4 is the ecosystem represented as a mosaic of functional domains. A functional domain is defined as the sum of structures produced by a given population of ecosystem engineers. It presents strong interactions, such as those between earthworms and roots. Indeed, earthworm casts are rich in readily available nutrients and can play a role in structuring plant communities.

Scale 5

At Scale 5, that of landscapes and the whole biosphere, delivery of ecosystem services (e.g. infiltration and soil water storage – hydrological services, see page 107) or climate regulation (see pages 102-106) through the storage of carbon in soil organic matter, is achieved through a set of rather complex interactions among all soil-living organisms, from microorganisms to megafauna, and the different types of ecosystems (e.g. forest and pasture).

Introduction

Biological and functional diversity

The relationship between soil biodiversity, functions and services has led to the distinction between two different types of diversity: biological diversity and functional diversity. [122]

Biological diversity

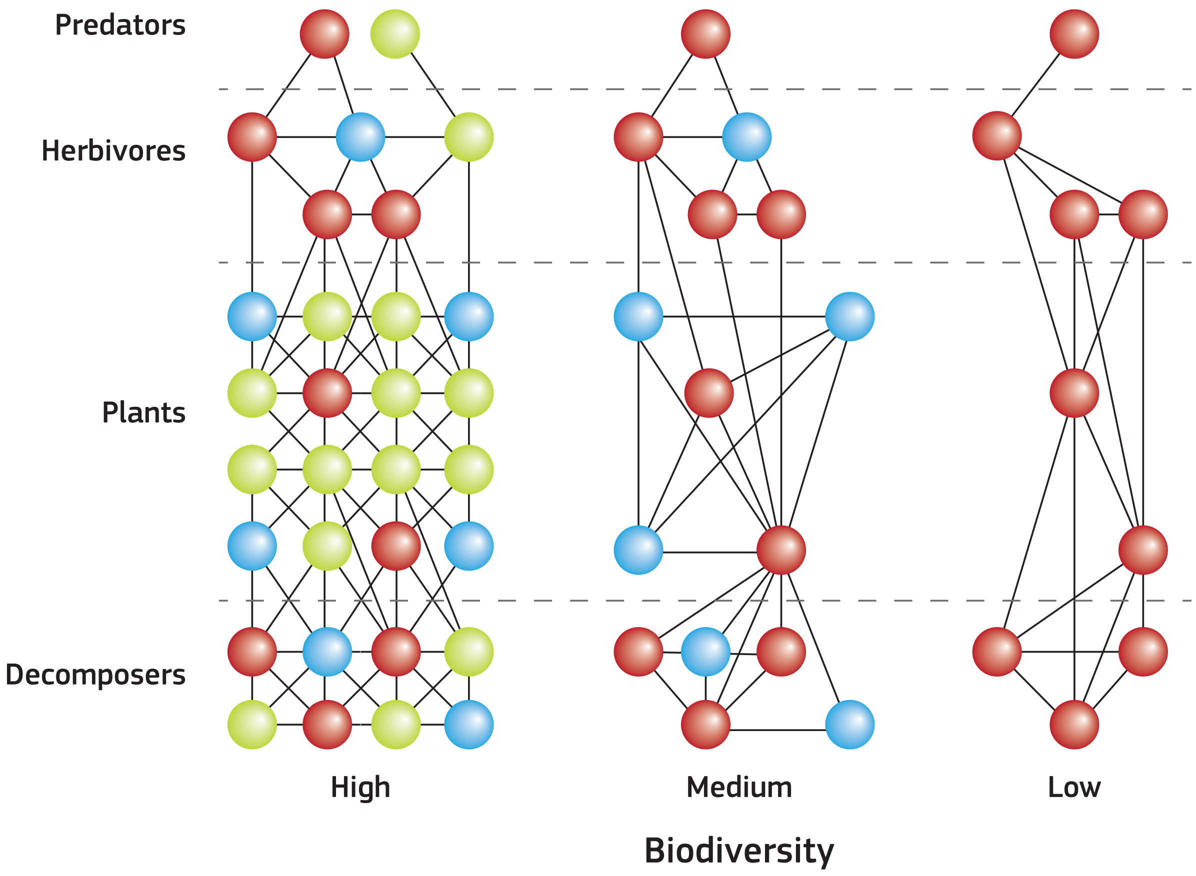
Biological diversity refers to the different species present in a community, including their genetic and intraspecific diversities. Here, the focus is on the number of species and, therefore, an ecosystem is considered to be biologically diverse when it contains species-rich communities.

Soils have a very high biological diversity. (**a**) *Megalanura tasmaniae*, a collembolan species from Tasmania and (**b**) *Trombidium grandissimum* a mite species from India. (AM, BG)

Functional diversity

Functional diversity is the diversity of roles that the soil community plays in a particular ecosystem. Soil organisms are commonly classified according to size (e.g. micro-, meso- and macrofauna, see page 31). However, it can be more informative to classify them according to the functional role they play in the soil, for example, as plant comminutors (that fragment litter), bioturbators (that mix soil) or mineralisers (that release nutrients). When organisms with the same functional ability occur together, this is referred to as 'functional redundancy' (see page 97).

Soil organisms have different functions. For example, (**a**) fungi are fundamental to litter decomposition and (**b**) moles mix soil through their burrowing activity and create large-sized pores. (JDR, NAL)



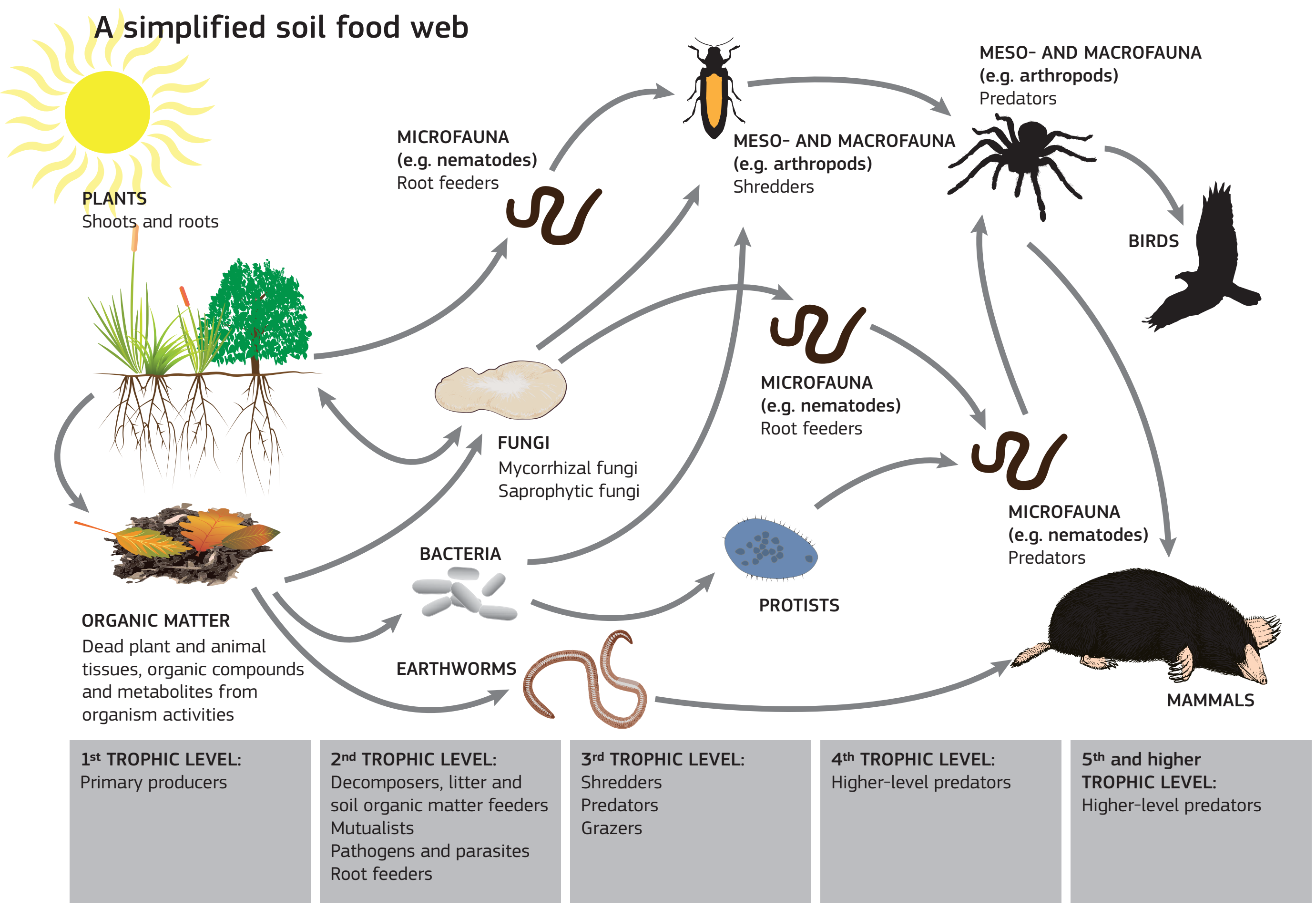
Soils host a complex food web, including predators, herbivores and decomposers, which scientists are still exploring. The trophic interactions among soil organisms are similar to what is observed aboveground between predators, herbivores, plants and decomposers. However, the compact and fragmented condition of the soil environment reduces the opportunity of organisms to interact with each other. (PL, JRC)

Interactions

Soil organisms, both as individual species and in groups, can interact with each other in either positive or negative ways; the more diverse the soil community, the more opportunity there is for interactions. Often in soils, these interactions are mutualistic, where the community members support each other's functions (see box on page 33). Understanding these interactions is important when considering the effect of drivers of global change, such as climate change, nitrogen deposition, pollution and urbanisation. These environmental stressors can significantly affect belowground communities, altering community composition and functioning. The consequence of community changes on soil functions is often difficult to quantify and predict, and there is reason for concern that changes in soil communities may negatively affect soil functions.

Trophic levels and food webs

- The trophic level of an organism is the position it occupies in a food web.
- Basal species, such as plants, form the first trophic level and feed on no other living creature in the food web. Species in this level are also known as primary producers, as they are able to convert solar energy or chemical energy into organic matter.
- The intermediate levels are filled with organisms that feed on more than one trophic level (predator-prey relationships) and transfer energy to the upper trophic levels through a number of food pathways, starting from a basal species.
- The uppermost trophic level includes top (or apex) predators that have no other species predating on them.



This simplified soil food web represents some of the possible feeding connections in a soil ecological community. The trophic level of an organism is the position it occupies in a food web. Soil formation parallels the development of a food soil web in that it is simple in the early stages and becomes complex during the mature stages of soil formation. (JRC)

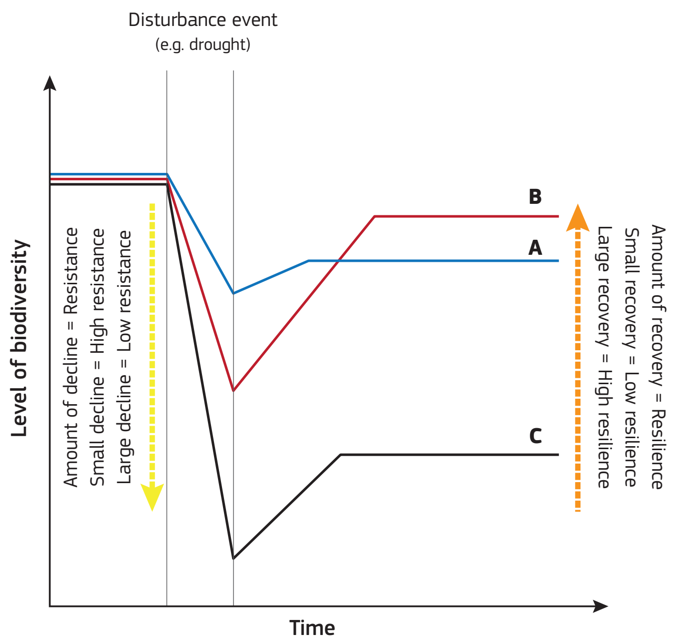
Functional redundancy

The role of soil organisms in supporting soil processes depends on the types of functions they carry out. However, more species do not necessarily equal more functions, or even higher rates of soil processes. This realisation lead to the coining of the term 'functional redundancy', a concept that describes a common characteristic of soils. Therefore, overlapping functions are an important component of community dynamics, and an important concept when considering global change effects on community composition and diversity. For example, higher functional redundancy can protect ecosystem services when the community is altered. For example, if an organism is lost or decreases in abundance due to a global change factor, another species carrying out the same functional role can ensure that the function will continue. The interactive nature of soil organisms, whether negative or positive, varies between systems and in response to different environmental stressors (see Chapter V). Many studies are now focusing on the influence that global change factors has on the response of soil communities and the potential consequences for soil functions. [123]

Resistance versus resilience

Associated with the concept of functional redundancy are the concepts of resistance and resilience. In fact, functional redundancy is often one of the reasons for high levels of resistance of soil communities to a given stressor.

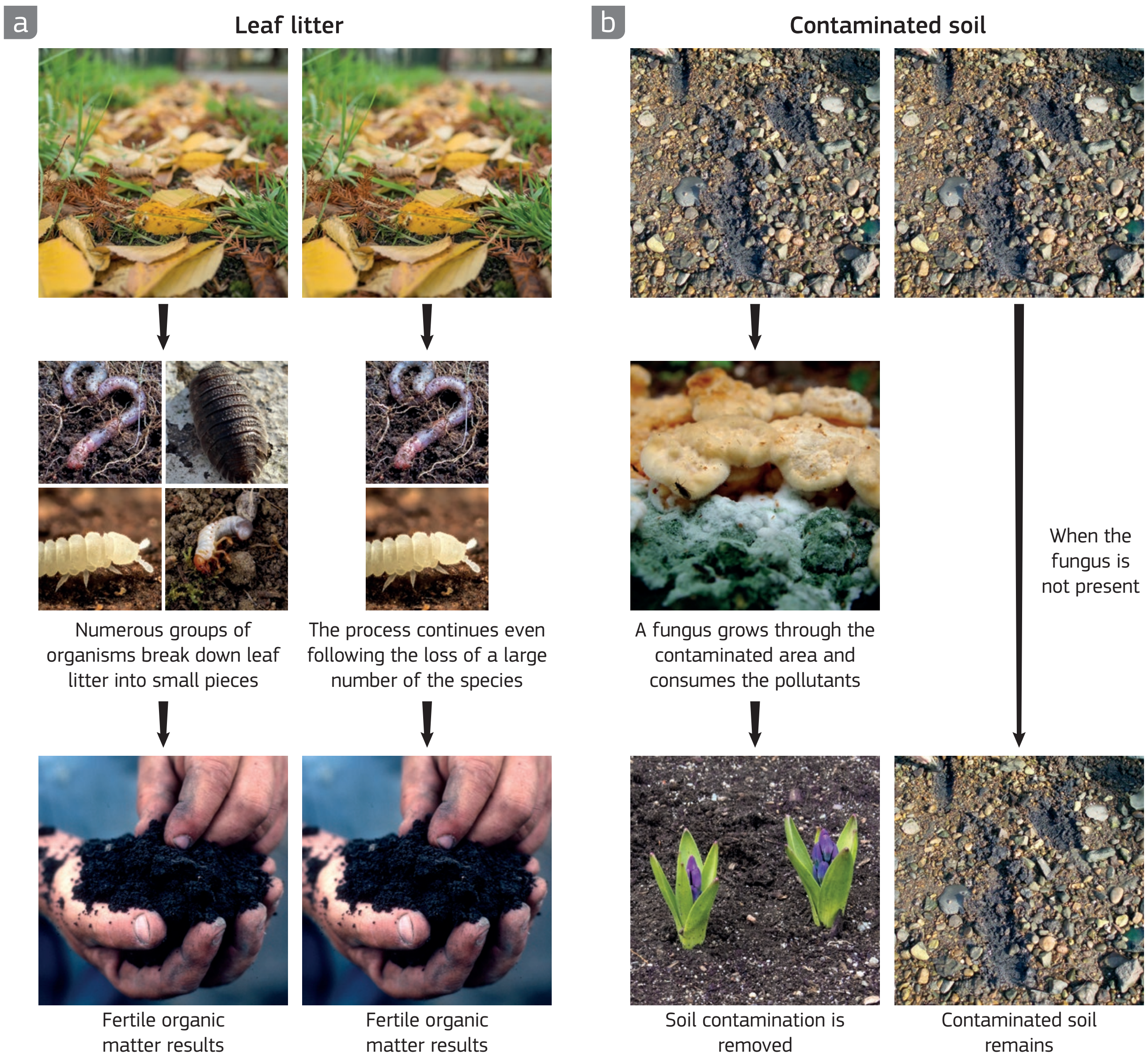
- resistance = how strongly a community can resist a stress without being negatively affected
- resilience = how quickly a community can recover after being negatively affected



The effect of a disturbance event on three different hypothetical soil communities. Community A shows relatively high levels of resistance but low levels of resilience, since it does not recover to pre-disturbance levels of functioning. Community B shows relatively low levels of resistance, but higher levels of resilience, and soon after the disturbance event is functioning again at pre-disturbance levels. Community C shows both low levels of resistance and resilience, and it is possible that the functioning of this community will be dramatically and permanently reduced after a disturbance. (PL)

As global change continues to increase pressure on soil biodiversity, it is becoming increasingly important to understand the resistance and resilience associated with different soil communities in order to conserve and optimise the ecosystem services they provide.

Pressures acting on soil, such as agricultural practices, can affect soil-living communities. The ability of a soil community to withstand pressure is known as resistance, while resilience determines the time needed to recover after a negative event occurs. (SME)



How functional redundancy works. (**a**) Many soil-living species function to break down litter into small pieces which microbes can convert through chemical activities. A loss of one species or group of organisms from the soil is unlikely to stop the process completely, although it may slow it down. (**b**) Other functions, such as the breakdown of pollutants, can only be performed by a few species, or potentially even only one species. Therefore, loss of this species or group of species will result in a complete loss of this function from the system. (JPE, PFL, MTA, AM, TGA, NRCS, MDEP, WSM, PMA)

Logging vs. microbial resilience/resistance

- Soil compaction is a major disturbance associated with logging in forests. It leads to oxygen and water limitations.
- A recent study investigated the resistance and resilience of soil microorganisms (bacteria and fungi) to this pressure. Fungi are less resistant and resilient than bacteria. [124]
- This can be explained by the generally higher sensitivity of eukaryotes (e.g. fungi, see page 30) to low oxygen pressures compared to prokaryotes (e.g. bacteria).
- Major changes in the microbial communities occurr in the medium-term, around 6-12 months after the disturbance. Four years after compaction, the community structure recovers in lightly compacted but not in heavily compacted soils.
- Soil microbial diversity may represent a powerful tool to measure the resistance and resilience of the soil system to compaction.

Soil compaction due to logging operations affects the resistance and resilience of soil microbial communities in forests. (CIFOR)

Many ecosystem services are supported by soil organisms and their interactions. The next pages of this chapter will highlight the most essential services that demonstrate the interconnectivity of the organisms and the underlying functions. Ecosystem services of each of the four classes (Provisioning, Regulating, Supporting and Cultural) will be presented; from the provision of food by increasing plant production, the regulation of climate, the support of the soil habitat to the cultural value associated with soil biodiversity.

Conclusions

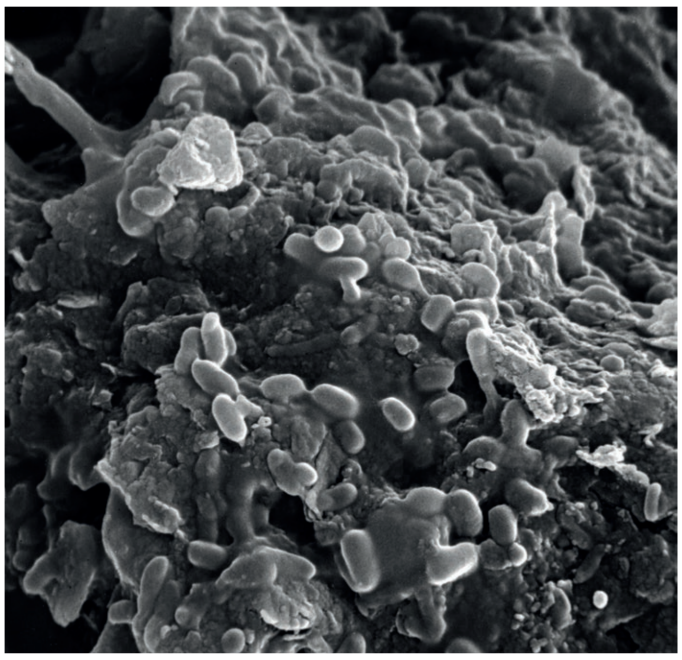
As global change continues to increase pressure on soil biodiversity, it is becoming increasingly important to know when to protect, conserve or optimise soil communities in order to conserve and optimise the ecosystem services we rely on. In fact, alterations in a group of organisms are likely to alter a function and resonate through the whole system.

Soil biodiversity is a major determinant of major ecosystem services, from plant growth and cultural value to the control of nutrient cycling and climate. The key roles played by soil organisms in providing benefits to humans is now well known. However, many of the ecological mechanisms responsible for these services are still unclear and are not easy to understand under the current changing global conditions. (RCR, JRC)

Provisioning services – Production of food and fibre

Soil biodiversity and plant production

Plants utilise associations with soil microorganisms in the same way that animals utilise gut and skin microorganisms to aid their digestion and resistance to diseases. The combined activities of the diverse array of cryptic soil organisms influence plant production and soil health. Recent advances in molecular genetics (see pages 64-65) have revealed a remarkable diversity of fungi and bacteria associated with plant roots (see Chapter II). Some of these microorganisms promote plant growth through enhancing plant nutrition. Other microorganisms increase plant fitness by protecting them from herbivores and pathogens. Some microorganisms also cause disease (see pages 108-109). [38]



Scanning electron micrograph showing a colony of bacteria on a humus aggregate. (TEI)

Mycorrhizal fungi

Mycorrhizas are ancient symbioses (see box on page 33) between plants and fungi. Fossils indicate that the earliest land plants hosted fungi in their tissues even before they evolved roots. Mycorrhizal fungi (see page 40) provide plants with necessary mineral nutrients and, in return, they obtain plant-derived sugars. Mycorrhizal symbioses are most beneficial in low-fertility soils because fine fungal hyphae can scavenge more efficiently for essential nutrients than plant roots could alone. The mutual advantages of these symbioses are clear from their tremendous diversity and abundance. Over 90 % of all plant species form at least one of the four major types of mycorrhizal symbioses: arbuscular mycorrhizas, ectomycorrhizas, ericaceous mycorrhizas and orchid mycorrhizas (see page 40).

There is a latitudinal pattern in the distribution of mycorrhizas in the Northern Hemisphere. Arbuscular mycorrhizas are dominant in warm tropical rain forests, grasslands, savannahs and deserts (see Chapter III). Ectomycorrhizas dominate temperate and boreal forests, and ericaceous mycorrhizas are common in boreal forests and heathlands. This pattern reflects the variation in the ability of different types of fungi to acquire essential nutrients from minerals and organic matter in the soil. In this regard, plants appear to associate with those types of fungi that can help them most efficiently to acquire nutrients from the soil environment. Mycorrhizas can also improve plant water relations by directly influencing water uptake or through indirect effects linked to plant nutrition, plant size and changes in soil properties.

Ectomycorrhiza formed by the fungus *Laccaria amethystina* and the roots of a beech tree (*Betula* sp.). (MB)

In addition to increasing plant nutrition, mycorrhizas influence plant production through their influence on soil formation and nutrient cycling. Some mycorrhizal fungi can enhance the weathering of soil parent materials (see page 20). In addition, mycorrhizal fungal mycelia stabilise soil aggregates and interact with other soil organisms by transporting plant-derived carbon compounds through the soil system. In fact, a large fraction of the organic matter in soil is represented by the mycelium of mycorrhizal fungi and, therefore, mycorrhizas account for much of the microbial carbon stored belowground.

Inoculation with efficient strains of mycorrhizal fungi has been shown to benefit the growth of many types of cultivated plants, especially in tropical systems and degraded soils. Mycorrhizal inoculum collected from the root zone of healthy soils, as well as commercially available mycorrhizal inoculum, have been used to enhance plant growth in forest nurseries, orchards and horticultural operations. Recent studies indicate that inoculation with mycorrhizal fungi together with myriad of other plant supporting organisms, such as nitrogen-fixing and phosphorus solubilising bacteria, may have a synergistic effect on plant growth. Individual plants generally host dozens of fungal species in their root systems. Human activities, such as agriculture, forestry and urbanisation can eliminate many beneficial mycorrhizal fungi from soils (see Chapter V); whereas earthworms greatly enhance plant infection by mycorhizas in agroecological production systems.

Although little is known about the functions of the many fungal species associated with plant roots, different species of mycorrhizal fungi are known to vary greatly in their effects on host plants. Furthermore, environmental conditions, such as high inputs of chemical fertiliser, can cause some species of mycorrhizal fungi to lose their beneficial effects, or even decrease the growth of their hosts. Consequently, caution should be taken when artificially inoculating plants with mycorrhizal fungi. Mycorrhizal inoculants are commercially available; however, their widespread application, especially in natural systems, is controversial because of unintended risks associated with the introduction of exotic species (see page 119). These potentially harmful effects on native communities can be minimised if the fungal inoculum is prepared using local strains of fungi.

(**a**) Coffee plant (*Coffea arabica*) and (**b**) Dutch clover (*Trifolium repens*) that are inoculated with arbuscular mycorrhizal (labelled as 1 and MYC) fungi are often larger and healthier than plants grown without mycorrhizas (2 and NO MYC). (IGI, OSJ, RBO, MTDB)

← Increasing latitude or altitude

Biome	**Heathland**	**Boreal forest**	**Temperate forest**	**Grassland**
Soil	Organic-raw humus (mor) or peat	Surface organic (mor-moder)	Brown earth (moder-mull)	Mineral
Nitrogen source	Organic-protein Little mineralisation No nitrification	Organic – NH_4 Limited mineralisation	NH_4 – NO_3 Mineralisation	NO_3 Nitrification dominates
Mycorrhizas	Ericoid (some Ecto-)	Ecto- (Ericoid understory)	Ecto- (Arbuscular understory)	Arbuscular (scarce Ecto-)
Fungal Symbiont Activity	Extensive abilities to degrade structural and nutrient-containing polymers	Considerable saprotrophic capabilities in both Ericoid and Ecto-fungi	Ecto-fungi of reduced saprotrophic capabilities AM fungi largely non saprotrophic	AM fungi with little or no saprotrophic abilities

← Decreasing soil pH

Decreasing phosphorus availability and P:N ratio →

General relationships between the distribution of the Earth's main biomes along environmental gradients and the roles of the prevailing mycorrhizal associations in facilitating N and P capture by characteristic functional plant groups (modified from Read and Perez-Moreno, New Phytologist, 2003). [125]

Bacteria and plant production

Many bacterial species that inhabit the plant root zone (rhizospere) have had beneficial effects on plant growth and productivity. These bacteria, called ‘plant growth promoting rhizobacteria’, help plants through several mechanisms, of which improved nutrition is one of the most important. [126]

Even though nitrogen is the most abundant gas in the air, plants cannot utilise nitrogen gas and their growth is frequently limited by a shortage of nitrogen. An estimated 97 % of the natural nitrogen inputs in terrestrial ecosystems are from biological nitrogen fixation performed by ‘nitrogen-fixing’ organisms. These organisms, scientifically known as diazotrophs, can convert nitrogen gas into a form of nitrogen that plants can utilise. Many plants benefit from associations with either symbiotic or free-living diazotrophs. Legumes are well known for their symbiotic associations with the nitrogen-fixing *Rhizobium* bacteria (see page 34) in distinctive root nodules. Other types of plants, such as trees of the genus *Alnus* (alder), form symbioses with nitrogen-fixing actinobacteria (see page 35) of the genus *Frankia*. The ability to form symbioses with *Frankia* appears to have evolved independently in at least three different orders of angiosperms. The majority of diazotrophs are not symbiotic but rather free-living inhabitants of the rhizosphere.

After nitrogen, phosphorus (see page 105) is often the most limiting resource for plants. Plants often associate with particular types of bacteria in their rooting zones to improve their access to phosphorus, which is often tightly bound to soil particles. Phosphorus solubilising bacteria include the *Rhizobium*, *Pseudomonas* and *Bacillus* species, along with many other aerobic and anaerobic bacteria. One of the major mechanisms by which these bacteria solubilise mineral phosphate is through the synthesis of organic acids, which causes phosphorus ions to be released from more complex molecules. The abundance, diversity and metabolic activity of nitrogen-fixing and phosphorus-solubilising bacteria and archaea are influenced by many factors, including soil chemistry, climate, plant community composition and land management.

Plant protection

Soil organisms also enhance plant production through their interactions with organisms that damage plants. For example, fungi (see pages 38-41) of the genus *Trichoderma* are known to prevent fungal attacks through a variety of complex mechanisms. A wide range of bacteria have similar effects. Earthworms (see page 58) also have recognised effects as control agents for parasitic nematodes (see pages 46-47). A rather diverse set of mechanisms may be implemented (e.g. accelerated eclosion of eggs in compact casts where nematode larvae will get trapped); destruction of nematode chemoreceptors during transit through earthworm guts by a proteolytic enzyme produced by specific bacteria; direct destruction of nematodes during the digestion process. Furthermore, researchers demonstrated that rice plants attacked by plant parasitic nematodes may become tolerant after earthworm activities have modified the expression of several genes in a way that allows plants to tolerate root grazing by nematodes.

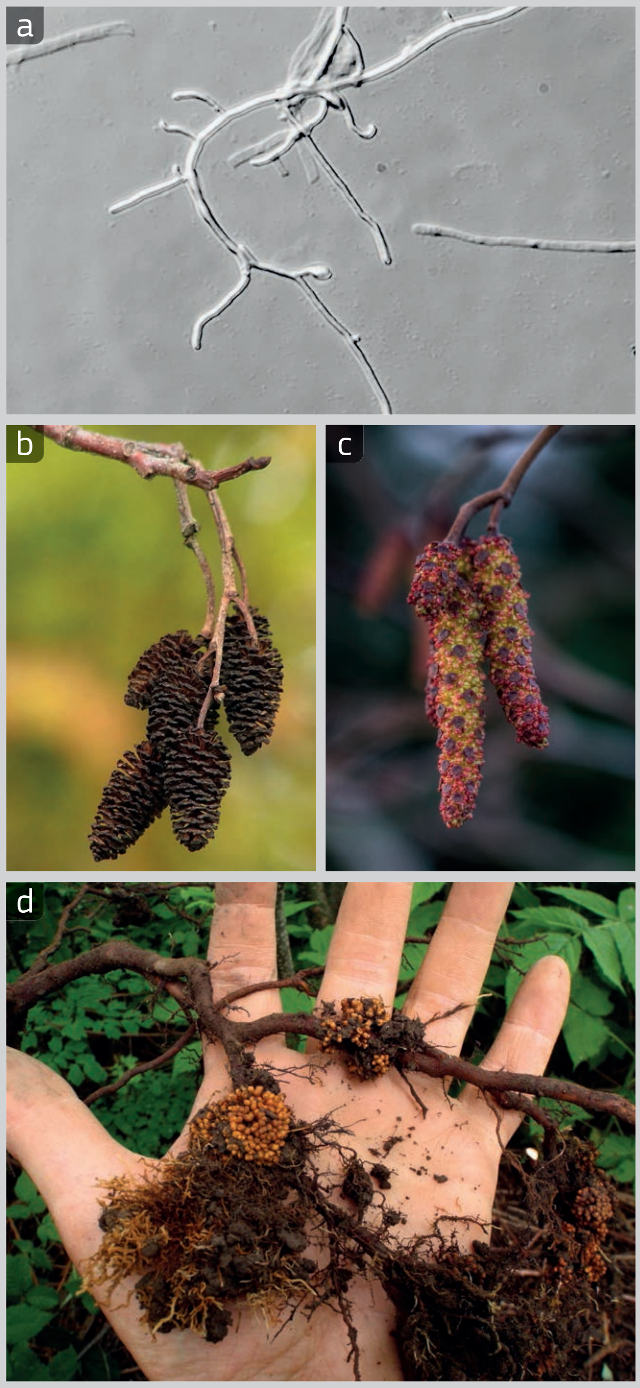
Rice plants with phytoparasitic nematodes are stunted and die; if earthworms are present, plants exhibit normal growth. (NP/CIAT)

Active antagonist relationships, predation and/or competition adjust community composition and abundance and may also help in conserving biodiversity. Food web controls in the plant rhizosphere are an example of such a process. Disturbances of natural or human origin may impair this dynamic equilibrium and produce uncontrolled multiplication of pests and disease agents. As a general rule, the simplification of the ecosystem and impoverishment of nutrient and organic matter reserves create conditions for these events by weakening plants' own defenses and the community of organisms that naturally limit the impacts of these aggressive agents. Therefore, these plant-soil interactions can improve plant production, and also provide many other ecosystem services (e.g. nutrient cycling – see pages 104-105), and should be considered when designing crop management to sustain productivity.

Rhizobacteria infect plant roots and establish symbiosis. (**a**) Transmission electron micrograph showing dark cells of the symbiotic *Bradyrhyzobium japonicum* within a plant cell. (**b**) The symbiosis develops specific structures, called nodules, at root level. (**c**) Leguminous plants, such as peas, can establish this type of symbiosis. (LH/DEMF, HRO, CLE)

The strange case of actinorhizal plants

- Actinorhizal plants are a group of angiosperms that form symbioses with the nitrogen-fixing actinobacteria of the genus *Frankia*, meaning that they convert atmospheric nitrogen into ammonia. This association leads to the formation of nitrogen-fixing root nodules.
- Actinorhizal plants belong to 24 genera and 8 families. Many are common plants in temperate regions, such as alder, bayberry and sweetfern.
- Actinorhizal plants are found on all continents, except Antarctica.
- Actinorhizal plants are the main contributors to nitrogen fixation in large areas of the world, and are particularly important in temperate forests.
- The symbiosis leads to root cell divisions and the formation of a new organ consisting of several lobes that are anatomically similar to a lateral root, known as actinorhizae.
- *Frankia* is a bacterial genus named after the German biologist, Albert Bernhard Frank, in 1886. *Frankia alni* is the only named species in this genus.



(**a**) A micrograph of the symbiotic bacterium *Frankia alni*. *Frankia alni* forms a symbiotic relationship exclusively with trees in the genus *Alnus* (**b–c**), commonly known as alder. (**d**) Alder roots with the typical actinorhizal nodules, i.e. actinorhizae. (LCA/KLB, PNO/KLA, NZL, AKR, RT)

Provisioning services – Biotechnology

Various groups of soil organisms have the potential to be manipulated and used for a wide range of environmental, commercial and industrial applications, many of which still remain largely unexploited. The use of soil organisms with the aim of generating a useful product or a desired metabolic process is generally known as 'biotechnology'. Such applications are possible thanks to three major soil biota traits:

a. their ability to break down substrates and to transform them into new compounds
b. their direct involvement in a multitude of biological processes
c. their high sensitivity to changes in the local environment

Of all soil organisms, microorganisms are particularly easy to cultivate (see pages 64-65) and to manipulate. Available microbial products in our everyday lives can be categorised as follows:

a. microbial cells that can be used as nutrients, immunising factors (e.g. vaccines) or clean-up agents (i.e. bioremediation)
b. enzymes and other macromolecules, synthesised by viable microbial cells
c. primary microbial metabolites, essential for cell growth and maintenance (e.g. amino acids)
d. secondary microbial metabolites, which are not essential for cell growth (e.g. antibiotics and steroids)

Each of these microbial products have important environmental, biomedical or industrial applications. Examples of such contributions are described below. [127]

Bioremediation

Remediation is the general term for any physical, chemical or biological process used to recover or restore ecosystem functions in contaminated or polluted soil or water. A particular case of remediation is bioremediation (see page 141), which takes advantage of biological activity ('bio') for the environmental clean-up ('remediation') of contaminants or pollutants, such as pesticides, metals and polycyclic aromatic hydrocarbons (PAHs). Bioremediation has been increasingly regarded as an alternative to the traditional physical and chemical treatments, as it generally has less undesirable impacts on the environment, and is often more cost-effective.

A broad range of environmental contaminants can be immobilised, metabolised into less toxic compounds, or mineralised via soil microbial metabolism. Such strategies can be used in one or more approaches (intrinsic bioremediation, biostimulation and bioaugmentation), depending on the contaminant type and concentration, the status of native microbial communities and the site-specific environmental and climatic combinations. Intrinsic bioremediation is carried out by native microflora and occurs naturally in contaminated environments, without the need for human intervention. However, in those cases where the local environmental conditions are not favourable for microbial metabolism, there are options to enhance the cleaning-up functions, such as through biostimulation of the native microbial degrading potential (e.g. addition of limiting nutrients, moisture, oxygen, etc.) or through inoculation of natural or custom-made selected species that exhibit specific metabolic features (bioaugmentation).

The fungus *Trametes versicolour* is a common inhabitant of temperate woods and a powerful remediation agent for numerous pollutants. (ACB, FVE)

Virtually, all groups of soil microorganisms (bacteria, fungi, viruses, algae and protists – see Chapter II) can be effective bioremediation agents. This process is also known to benefit from the activity of other larger organisms that can contribute to enhancing the surrounding microbiome, including terrestrial invertebrates, such as earthworms and isopods (see pages 56, 58). Interestingly, some white-rot fungi can be 'tricked' into co-metabolising a contaminant in the presence of suitable lignocellulosic substances (e.g. sawdust, woodchips, straw, etc.), which are their usual substrates for growth and development. This is the case of the white-rot species *Trametes versicolour*, a common inhabitant of temperate forests and decaying wood.

Plants can also be used for immobilisation and extraction of contaminants from soil, including heavy metals. This particular case of bioremediation is commonly referred to as phytoremediation. In this process the plant does not normally use the contaminant as a nutrient. Rather, the plant gradually builds up the contaminant in the shoot and/or leaves, and sometimes in the roots, in a process parallel to its own development. Plant-accumulated metals can then be recovered using specific extraction processes, which in some cases can be more cost effective than traditional metal recovery procedures. In a phytoremediation experiment, the potentials of the ribbon (*Pteris cretica* 'Wimsettii') and brake (*Pteris vittata*) ferns to hyperaccumulate arsenic were tested in contaminated hydroponic media as well as in contaminated soil, in the vicinity of a former tin mine. It was found that *P. vittata* and *P. cretica* 'Wimsettii' could accumulate up to 12 mg and 3 mg of arsenic per plant, respectively, when grown in soil contaminated with this element. The selection of the suitable organism (or group of organisms) for any given bioremediation strategy is the key step for the successful removal of pollutants and will depend mainly on the chemical properties of the contaminant to be removed from the environment.

The ferns *Pteris cretica* 'Wimsettii' (ribbon fern) and *Pteris vittata* (brake fern) one week after being transplanted into arsenic-contaminated soil, show their ability to live in contaminated soils and, thus, be used for bioremediation purposes. (SSW)

Agricultural revolution

The Green Revolution was started in the late 1940s by the American biologist Norman Borlaug. Research coupled with technological development allowed for an increase in agricultural production. The basis of the Green Revolution largely arose from the development of technologies, such as synthetic nitrogen fertiliser, pesticides and modern irrigation techniques, combined with the production of novel cultivars, particularly wheat, maize and rice. Such cultivars were created through conventional breeding methods. While a great success in terms of increased productivity and, therefore, increased global food security, the Green Revolution was, unfortunately, not without its negative impacts. In fact, intensified land use in agriculture and forestry is sometimes considered the main cause of biodiversity loss. Biodiversity has been reduced because of the reliance on just a few high-yielding varieties of each crop. Extensive use of pesticides is generally required due to this switch to monocropping systems.

By 2050, the global population is projected to be 50 % larger than at present, and global grain demand will most likely double. Therefore, further increases in agricultural yields are essential for global political and social stability. However, the simplification of agroecosystems caused by the intensification of agricultural practices may affect important ecosystem functions via the loss of biodiversity, such as plant growth, pest control, pollination and decomposition processes.

In recent years, aiding pollination in some agroecosystems has resulted in reduced blossom drop and improved fruit set, leading to enhanced crop yield and quality (e.g. tomato growers). For example, the use of artificial beehives containing functional bumblebee (*Bombus terrestris* – see box on page 61) colonies or other natural pollinators has expanded to a range of other crops, particularly in greenhouses, where artificial lighting, often inadequate ventilation, coupled with limited access for pollinators may compromise sufficient pollen transfer.

Genetically modified organisms

A range of genetically modified organisms (GMOs – see box on page 123) used (or proposed for use) in agriculture have been produced through biotechnology. These include both pest- and herbicide-resistant plants, as well as crops with augmented nutrient contents, such as golden rice, each of which are discussed in more detail below. The production and use of GMOs is not without controversy, and they are still heavily regulated in some parts of the world, including in Europe, but much less so in other parts, such as Africa and North and South America.

One of the most widely used forms of genetically modified crops is referred to as 'Bt crops'. These are crops that have been engineered to express genes from the soil bacterium *Bacillus thuringiensis*. The plants produce the Bt toxin, which functions as an insecticide, thus helping to protect the crop from insect pests. Such crops have been widely adopted in some countries, mainly the USA, Brazil, Argentina, India and Canada, where they have been associated with a reduction in pesticide use and, consequently, with environmental and economic costs. However, resistance to the first generation of Bt cotton was reported to have arisen in a pest known as the pink bollworm, in 2009. This led to the production of a second generation of Bt crops which have multiple Bt proteins to overcome the problem of resistance. It has been reported that the pest communities that affect such crops are changing, with an increase in the prevalence of pests with sucking mouth parts, which are not affected by the Bt toxins. Clearly the battle against crop pests is far from won.

Another type of GMO that is often used in agriculture is herbicide-resistant crops. The most commonly used varieties of these are Roundup Ready soybean and maize. The gene used for the modification was derived from a soil species of the bacterial genus *Agrobacterium*. Such plants are resistant to glyphosate, allowing its use to reduce weed species in crop fields, thereby increasing yields.

Another genetic modification proposed for use in agriculture is the augmentation of the nutritional value of a given crop. One such example is 'Golden Rice'. This rice has the genes for the production of beta-carotene (a precursor of vitamin A which is usually absent in rice), with the aim of countering the dietary deficiency of vitamin A (see box on page 115). One of the two inserted genes (carotene desaturase – CRTI) is from the bacterium *Pantoea ananatis* (previously known as *Erwinia uredovora*).

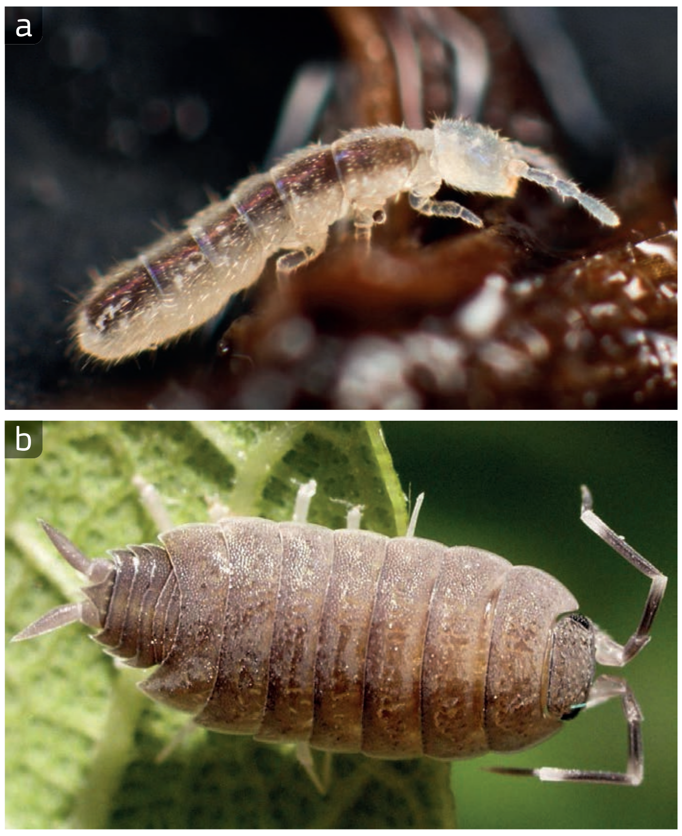
The application of biotechnology to agriculture is largely debated, and further research into both the positive and negative effects is required. The consequent adoption of agricultural production and management practices based on biotechnology may contribute to abating some of the negative consequences of the Green Revolution.

(**a**) Crystals of the Bt-toxin from *Bacillus thuringiensis*. This protein is produced by GM plants and has insecticide effects on some pests, such as (**b**) the lepidopteran species *Ostrinia nubilalis*. (JBU, DHO)

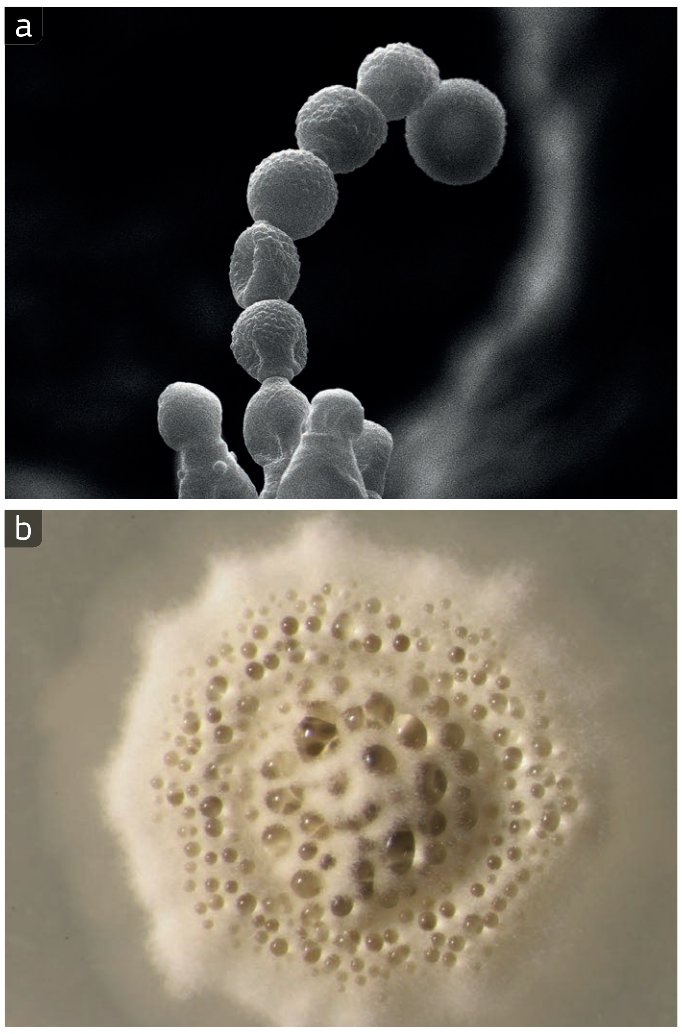
Biopharmaceutical and biomedical applications

Complex interactions between soil organisms, such as avoiding predation and competing for food and space, has led to the evolution of a range of mechanisms that allow organisms to gain advantage, in both attack and defence. One of these is the secretion of chemical substances with antibacterial/antifungal (i.e. kills bacteria or fungi) or bacteriostatic/fungistatic (i.e. inhibits growth of bacteria or fungi) properties. These are known as antibiotics. [128]

Chemicals of microbial origin can be isolated and used as antibiotics; these include the well known penicillin (isolated from the soil fungus *Penicillium chrysogenum*) and semi-synthetic derivatives, as well as amynoglicosides (e.g. streptomycin, kanamycin), lipopeptides (e.g. daptomycin) and tetracyclines (all isolated from soil actinomycetes (see page 35), such as *Streptomyces* spp.). Besides antibiotics, other valuable therapeutic agents and supplements may be found in soil organisms. Steroids and other hormones, as well as biologically active forms of amino acids (e.g. lysine, glutamic acid, tryptophan) are also common products of microbial synthesis by either naturally occurring or genetically engineered soil microorganisms. In recent years, some microbial secondary metabolites (e.g. red pigments) have also been discovered that exhibit potential anti-tumour and cholesterol-lowering activity, with potential anti-carcinogenic and cardiovascular benefits, respectively.



Examples of representative soil organisms that are commonly used as indicators of environmental changes: (**a**) the blind and white-pigmented collembolan *Folsomia candida*; (**b**) the terrestrial isopod *Porcellionides pruinosus*. (AM, FTG)



(**a**) Spores of *Penicillium chrysogenum*, the fungus from which penicillin was isolated. (**b**) A colony of *Streptomyces* spp., a genus of Gram-positive bacteria known for producing many antibiotics. (ABH/EAC, ADO)

Bioindicators

Most soil organisms are sensitive and respond quickly to changes in their environment. This trait makes them ideal (bio)indicators of environmental and ecological changes. Such change may compromise soil quality and/or ecosystem functions or specific ecological processes, and may result from natural or anthropogenic stressors, such as contamination and pollution. Bioindicators can be classified into three main categories, which are not mutually exclusive: 1) early-warning indicators of local environmental changes (environmental indicators); 2) monitoring tools for specific ecosystem processes and threats (ecological indicators); and 3) indicators of species richness (biodiversity indicators). While traditionally the inclusion of biological indicators in soil monitoring programmes has been only minimally considered, the substantial indicator potential of the soil biota (including abundance, diversity and biological function) is now increasingly recognised in order to complement soil quality assessments, site-specific management strategies or progress monitoring of ecosystem recovery and restoration.

Example of microbial product or application	Representative producing microorganism	Additional comments and conditions
Antibiotics (e.g. penicillin and related ß-lactams, streptomycin, cephalosporin, etc.) and antimalarials	*Penicillium chrysogenum* (F), *Streptomyces griseus* (B) and *Acremonium chrysogenum* (F)	Antibiotics are the most popular among the pharmaceuticals produced by soil microorganisms. *Streptomyces* and *Penicillium* together produce more than half of the antibiotics used worldwide
Steroids and human-growth hormones	*Rhizopus nigricans* and *Rhizopus arrhizus* (F)	Cortisone, hydrocortisone and aldosterone help regulate the levels of serum glucose, as well as sodium and potassium. Rhizopus is used as a mediator in the bioconversion of progesterone into cortisone-related compounds
Antitumour, immune-suppressive and cholesterol-lowering activities	*Pleurotus ostreatus* (F), *Aspergillus terreus* (F), *Serratia* spp. (B), *Streptomyces griseoviridis* (B), *Vibrio psychroerythrus* (B)	Lovastatin and the semi-synthetic Simvastatin are cholesterol-lowering drugs produced by the soil fungi *Pleurotus ostreatus* (commonly known as the 'oyster mushroom') and *Aspergillus terreus*, respectively. Both drugs were also found to be powerful immune-suppressants of great antitumour potential, as approved by the Food and Drug Amministration of the United States. Microbial red pigments (prodigiosins) produced by certain *Serratia*, *Streptomyces* and *Vibrio* species are also believed to have anti-tumour properties
Vitamins (e.g. riboflavin – vitamin B$_2$, cobalamin – vitamin B$_{12}$, and ascorbic acid – vitamin C)	*Streptomyces olivaceous* (B), *Pseudomonas denitrificans* (B), *Bacillus megatherium* (B), and some species of *Gluconobacter* (B)	Generally, vitamins are not synthesised in sufficient amounts by higher organisms, although they are metabolically essential to all. Vitamins have relevant applications in a range of sectors (e.g. food and feed, pharmaceutical, cosmetics, etc.)

Main soil bacteria (B) and fungi (F) that are used for the production of compounds with pharmaceutical and therapeutic applications.

A number of soil invertebrate groups can be used as bioindicators, including earthworms, enchytraeids, terrestrial isopods and collembolans (see Chapter II). Plant species, such as the turnip (*Brassica rapa*), oats (*Avena sativa*) and lettuce (*Lactuca sativa*), can also be used for their bioaccumulating capacity to detect pollutants in soil (see page 141). The choice of a bioindicator depends on the specific application or threat and the ecosystem of interest. Acceptance of the involved methodology and measurability and costs are generally additional criteria to be considered. However, even within the same system, different microhabitats (e.g. litter layer, foliage, etc.) may be subject to different environmental or ecological changes. Therefore, litter dwellers (e.g. ants and termites, centipedes and millipedes, snails and other molluscs, ground beetles – see Chapter II) or foliage inhabitants (e.g. ants and some groups of leaf beetles, moths and spiders) may also be selected accordingly.

Future prospects and expectations

Although the term is relatively new, the concept of 'biotechnology' has existed for thousands of years in the leavening of bread, brewing and other fermentation processes (e.g. in the making of cheese, beer and wine), as well as in direct interventions in animal and plant breeding in farm and agricultural systems. Industrial biotechnology involves industrial-scale processes, such as food and feed processing, manufacturing a range of products and materials, from flavour enhancers to solvents, biofertilisers, biocontrol agents and sources of bioenergy. Due to its large unknown component, soil biodiversity is likely to be an important source of new products for such industrial purposes.

Currently, the scale at which biotechnological production is required in order to meet societal, commercial and industrial requirements is enormous. In order to ensure such feasibility, the target organism (e.g. bacterium) must be able to grow quickly and cheaply, while producing the desired compound (e.g. drug) in large quantities, in ways that are easy and cost-effective to isolate and, subsequently, to recover and purify. Such organisms are hard to find and, considering the vast diversity of life in soils, we are just beginning to scratch the surface.

Along with global climate change and over-population, new challenging targets and refreshing prospects are expected from industrial and environmental biotechnology, whether in terms of impact, mitigation or adaptation strategies. The impacts of such environmental and societal pressures reflect on agriculture, land-use and water supply and, consequently, on the availability of food, energy and fresh water. Adaptation strategies may rely on new and improved crop varieties, with higher nutritional value and increased resistance to drought, pests and diseases, as well as on the exploitation of alternative food products, biomass and bioenergy sources and effective water purification strategies. Contributions to mitigation of the stressors can arise in the form of new or improved biomass conversion and renewable energies, carbon and greenhouse gas sequestration measures, and more effective waste management options.

Restoration of vast sand banks to promote habitat and biodiversity recovery in Central Portugal, as an example of new applications in which soil biodiversity could play a key role. (MSN, RMO)

Due to their great diversity, soil organisms offer a lot of resources that are already available, especially in soils with suitable biological, chemical and physical properties. The wealth of natural capital must be further investigated in order to preserve it and evaluate the range of possible applications. Given the many challenges we must overcome to achieve sustainability in light of global climate change and overpopulation, it is vital that we explore the breadth of the options that soil biodiversity provides. Soil biodiversity will be a vital cog in the machine of many adaption and mitigation strategies.

Regulating services – Atmospheric composition and climate regulation

Climate change

Climate change is most likely the greatest challenge that humans will face this century. The role of microbiota in determining the Earth's atmospheric composition, and hence climate, started with the origin of life. From the first molecules of oxygen produced by marine cyanobacteria 3.5 thousand million years ago, to the production of methane by archaea (see page 32) in the warm, carbon-rich swamps of the Carboniferous period, microbial processes have long been key drivers of, and responders to, climate change. Throughout the history of our living planet, microbes have been the main modulators in determining atmospheric concentrations of greenhouse gases (GHG), including carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O). [129]

Carbon dioxide

The amount of CO_2 in the atmosphere is determined by the balance between photosynthesis (see box on page 35), which consumes CO_2, and respiration, which produces CO_2. It is estimated that ~120 thousand million tonnes of CO_2 are removed from the atmosphere by photosynthesis each year. This is approximately balanced by ~119 thousand million tonnes emitted into the atmosphere by autotrophic (plant – see page 43) and heterotrophic (microbial) respiration.

Soils can act as either a source or a sink of atmospheric carbon. Globally, soils contain a vast amount of organic carbon (~1 550 thousand million tonnes), which is more than the total carbon contained in vegetation and the atmosphere combined. An additional 750 thousand million tonnes of carbon is contained in inorganic forms in soils. These soil carbon stocks are not static, but dynamic over time, with accumulation occurring through plant and animal inputs, and losses via decomposition of soil organic carbon (SOC) leading to the release of CO_2 into the atmosphere. Agriculture and other land-use changes, such as deforestation, that cause soil disturbance, greatly accelerate the decomposition of SOC and thus increase net emissions of CO_2 to the atmosphere. Since industrial activities began (1760-1840), it has been estimated that 40-90 thousand million tonnes of SOC have been released. This is significant considering that the release of 1 thousand million tonnes of soil carbon can result in a 0.5 ppmv (parts per million by volume) increase in atmospheric CO_2.

Soil biodiversity plays both a direct and an indirect role in the flux of carbon (C) to and from the soil. Through the decomposition of organic matter (see page 106), the soil biota are responsible for the release of 60 thousand million tonnes of C via heterotrophic respiration each year. Indirectly, through the regulation of the supply of nutrients (nitrogen, phosphorus and micronutrients – see pages 104-105) that are essential for plant growth, the soil biota influence plant growth and, thus, affect the removal of CO_2 from the atmosphere. There is sufficient evidence to suggest that increasing soil erosion alone could switch the soil from being a sink for carbon to being a source of carbon. The soil biota play a key role in the prevention of soil erosion and, thus, carbon loss through the production of sticky polysaccharides and fungal hyphae that physically bind the soil particles together and limit the susceptibility of soils to erosion (see box on page 149).

Methane

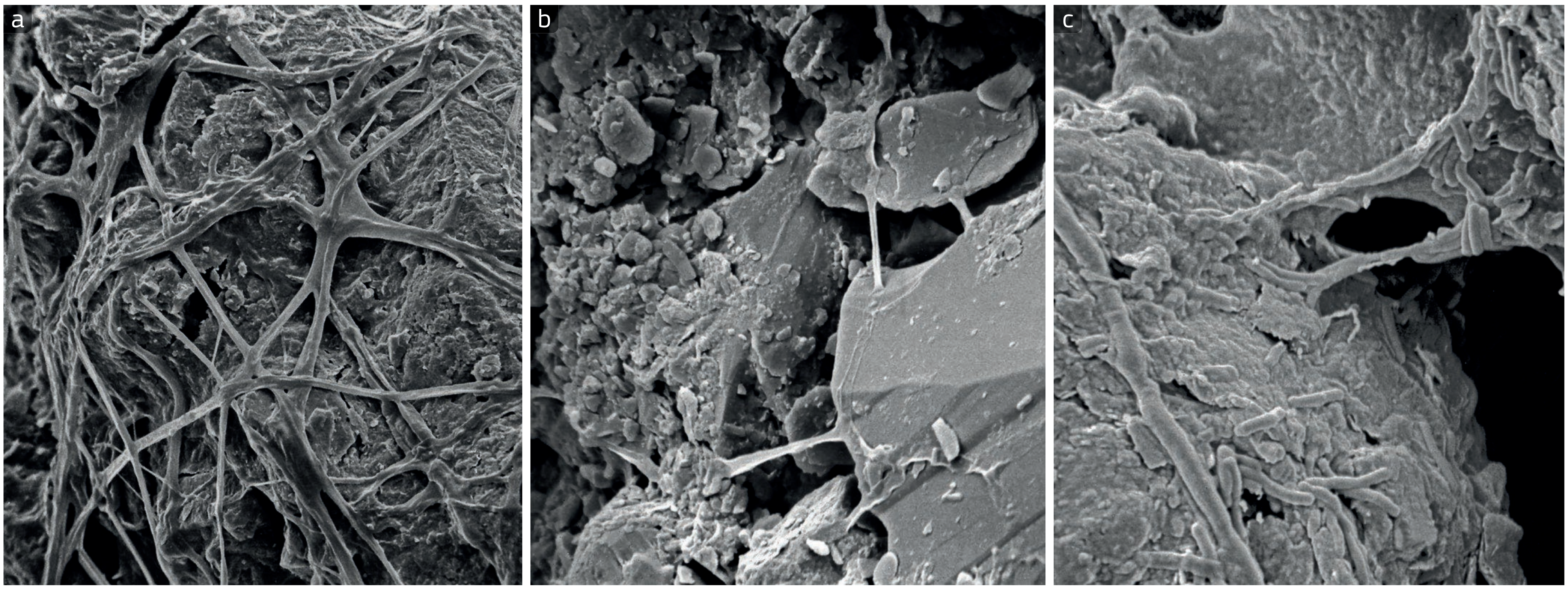
Methane (CH_4) is the second most important greenhouse gas, with a global warming potential (GWP – see box on page 103) estimated to be 25 times higher than that of CO_2. Terrestrial CH_4 emissions are under even greater microbial control than that of CO_2. Natural emissions (~250 million tonnes a year) that primarily (~95 %) originate from terrestrial ecosystems, including natural wetlands, result from the activity of a group of microbes known as archaea (see page 32) through the process of methanogenesis. Soil arthropods (see Chapter II) contribute ~20 million tonnes of CH_4 every year. These are exceeded by anthropogenic emissions (~320 million tonnes per year) from rice cultivation, livestock farming, landfill and fossil-fuel extraction that (with the exception of fossil-fuel extraction) promote abundance and activity of methanogenic biota.

Most of the atmospheric CH_4 is removed by chemical reaction. Nevertheless, a considerable amount (~30 million tonnes per year) of atmospheric CH_4 is consumed by specific soil bacteria through the process of methanotrophy. Additionally, soil bacteria consume between 50 and 90 % of the CH_4 produced in soils. Ultimately, biological removal of atmospheric CH_4 determines whether the terrestrial ecosystem is a net sink for or source of CH_4. Because of the strong biological control of methanogenesis and methanotrophy, soil microbiota are key regulators in the CH_4 flux to and from the atmosphere.

Soil fungi and carbon storage

- Soil is one of the Earth's main carbon sinks. Soil organic matter contains approximately three times as much carbon as the atmosphere.
- Mycorrhizal fungi (see page 40) are important regulators of soil organic matter.
- Researchers have demonstrated that ecosystems dominated by trees that form relationships with ectomycorrhizal (EM) fungi store about twice as much carbon as systems in which arbuscular mycorrhizal (AM) fungi dominate. [130]
- Differences in the soil bacterial community can also be an important determinant of soil carbon sequestration. It has been reported that soil profiles dominated by specific phyla (acidobacterial) store more carbon compared to soil dominated by Proteobacteria (see page 34).
- This mechanism could be regulated by nitrogen availability. High levels of N availability can reduce microbial mining of soil organic matter and, thus, promote soil carbon storage.
- Free-living soil microbes influence climate warming by increasing the carbon dioxide respired from soils into the atmosphere. This effect is smaller in EM-dominated forests and acidobacterial dominated soil profiles.
- Another explanation might be that trees in these ecosystems allocate more carbon belowground in order to satisfy the greater demands of soil microbes.

Methane emissions are partially caused by soil biodiversity. However, anthropogenic activities, such as (**a**) livestock farming, (**b**) landfill and (**c**) rice cultivation, are responsible for most global emissions of methane. (USDA, NBO, MHI)



(**a**) Fungal hyphae and (**b-c**) bacterial filaments form net-like structures that can stabilise soil particles. This allows for the stabilisation of soil and helps limit the susceptibility of soil to erosion and, thus, the loss of carbon. (TEI)

Nitrous oxide

The flux of nitrous oxide (N_2O) from terrestrial ecosystems is predominately biologically controlled through the processes of nitrification and denitrification. Global emissions of N_2O, which has a GWP 298 times that of CO_2, are estimated to be 19 million tonnes per year, 36 % of which is attributed to anthropogenic activities, mainly from agriculture.

About 55 % of natural emissions, and most of the anthropogenic emissions, are released from terrestrial ecosystems. Most of the N_2O produced by nitrification results from the activity of ammonia-oxidising bacteria and archaea (AOB and AOA, respectively – see pages 32-35). Denitrification is a multi-step process in which each step is carried out by a distinct group of microbes widely distributed across diverse phylogenetic lineages. It is estimated that for every tonne (1 000 kg) of reactive nitrogen deposited on Earth, 10-15 kg are emitted as N_2O through nitrification and denitrification (see page 105). The substrates for N_2O production (ammonium and nitrate) enter soils via natural biological nitrogen fixation, chemical fixation (lightning and fertiliser production), rainfall, or from the decomposition of plant and animal waste.

Nitrogen can enter the soil through animal waste; for example, sheep excrements are nitrogen-rich because of the grasses that they consume. (AO)

Climate change and feedback responses

There is limited evidence available as to whether the feedback response of climate change will increase (positive feedback) or decrease (negative feedback) GHG emissions. Current evidence suggests that global warming will positively influence the physiological response of the soil biota, and lead to increased decomposition of SOC, resulting in higher respiration rates and levels of CO_2 released into the atmosphere. Similarly, increased microbial activity could lead to increased CH_4 and N_2O emissions from the soil. However, the extent of such increases in GHG emissions under future climate conditions is widely debated, and estimates are accompanied by large uncertainties. Indirectly, soil biota can influence photosynthesis (see box on page 35) through regulation of the supply of essential nutrients to plants. Under future climate scenarios, the rate of photosynthesis is predicted to increase through warmer temperatures, longer growing seasons and higher CO_2 concentrations. However, this can only be sustained if other nutrients are cycled at an accelerated rate in order to satisfy increasing plant demands for nitrogen, phosphorus and other micronutrients, which will be largely determined by the activities of soil biota.

While microbiota and plants are the main contributors of natural GHG emissions, feedback responses and mitigations, the role of soil dwellers, such as earthworms (see page 58), insects (e.g. ants and termites – see pages 54-55) and small mammals (e.g. moles and rodents – see pages 62-63) is important for the formation of the soil structure (i.e. large pores and tunnels) that directly influence gas permeability and the activity of the microbiota responsible for the abovementioned functions.

The strong correlation between increased human-mediated soil disturbance and increased GHG emissions is clear, but a better understanding of how soil management affects microbial-mediated processes and biodiversity will serve to design management practices that minimise the impacts of future climate conditions on GHG emissions.

Greenhouse gases and their effects

- The greenhouse effect is a process by which thermal radiation from the Earth's surface is absorbed by atmospheric gases, and is re-radiated in all directions, resulting in an elevation of the average surface temperature above what it would be in the absence of the gases.
- The most abundant greenhouse gases in the Earth's atmosphere are:
  - water vapour (H_2O);
  - carbon dioxide (CO_2);
  - methane (CH_4);
  - nitrous oxide (N_2O).
- The concept of Global Warming Potential (GWP) was developed to allow comparisons of the global warming impacts of different gases. Specifically, it is a measure of how much energy the emissions of one tonne of a gas will absorb over a given period of time, relative to the emissions of one tonne of carbon dioxide. The larger the GWP, the more that a given gas warms the Earth compared to carbon dioxide over that time period, usually 100 years. GWPs provide a common unit of measure.
- Therefore, carbon dioxide has a GWP of 1. The GWP of methane and nitrous oxide over 100 years is 25 and 298, respectively. Calculation of the GWP of water vapour is complex as its concentration in the atmosphere depends on air temperature and water availability.
- Venus's climate is strongly driven by the most powerful greenhouse effect found in the Solar System. The greenhouse gases sustaining it are water vapour, carbon dioxide and sulphuric acid aerosols.
- On Venus, about 80 % of the incoming solar radiation is reflected back into space by the cloud layer, 10 % is absorbed by the atmosphere, and only 10 % gets through to heat the surface. However, the radiation emitted by the surface gets trapped by GHGs and results in an amazing 500 °C difference between the surface and cloud-top temperatures.

Mitigation

While biota act as a source of GHGs, they can also play a major role in mitigation, through careful manipulation and management of soils. Switching land uses (from arable to forestry) or management practices (from tillage and high input of nitrogen fertilisers to a no-tillage and low input system – see Chapters V and VI), where appropriate, will lead to low energy decomposition pathways, dominated by fungal communities and oligotrophic bacteria (see pages 33-35), favouring slower rates of carbon turnover and less CO_2 being released from soils. Such a conversion would also reduce CH_4 flux. Furthermore, it has been proposed that an annual increase of 0.004 % of C stored in soils (4 grammes of carbon for every 1 000 grammes of carbon currently stored in soils) would almost completely neutralise the predicted increase in GHG emissions, thus allowing countries to remain within the +2 °C limit in atmospheric warming. Practically, this increase would only be achievable in managed soils, resulting in less mitigation potential because of the emissions associated to the management practices; however, the issues clearly demonstrate the importance of preserving and increasing soil carbon stocks.

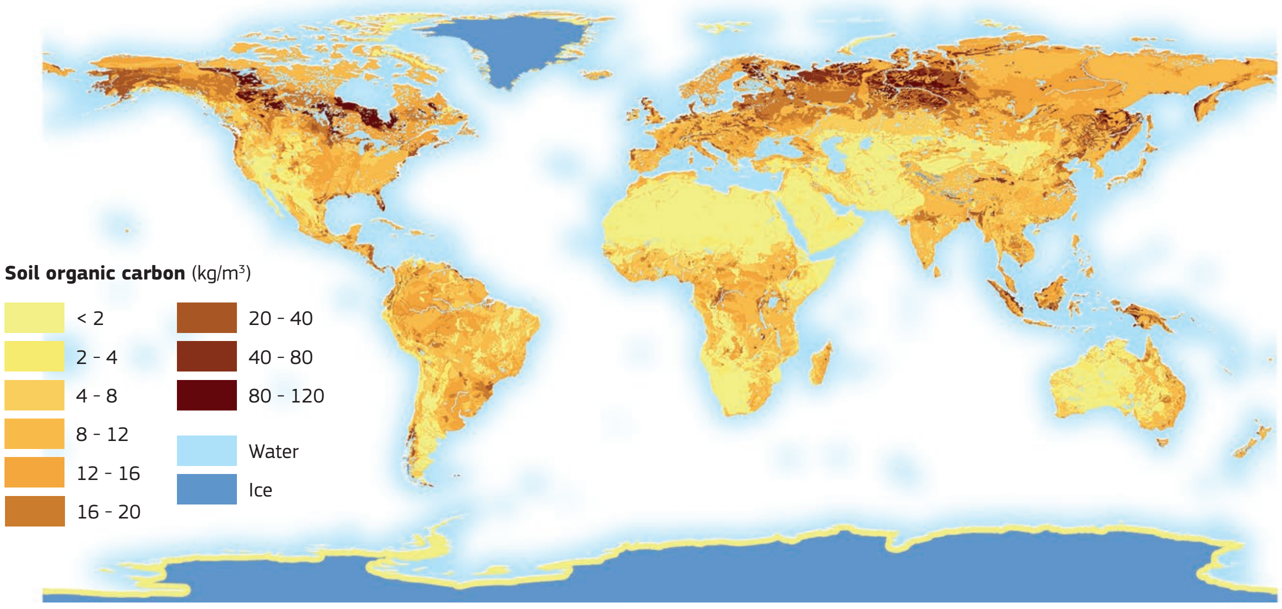
In agriculture, reduced-tillage practices (see pages 146-147) support the activities of earthworms and other soil fauna as well as fungal communities, and promote C sequestration and nitrogen (N) cycling. Similarly, the conversion of croplands into permanent pastures and the manipulation of plant diversity could be used to reduce the amounts of carbon released from soils. Improved management of flooding frequency in rice cultivation would increase oxygenation and reduce CH_4 emissions, as may the use of effective inhibitors of methanogenesis. Similarly, using nitrification inhibitors can limit denitrification and N_2O emissions. In addition, to improve drainage and limit denitrification, changes in land management have a great potential for further reducting N_2O emissions through the use of slow-release fertilisers and, subsequently, decreasing in the amounts of nitrate that are likely to result in N_2O emissions.

Climate change mitigation may be facilitated by changing how the land is used. For example, moving (**a**) from a tilled to an untilled agricultural field or (**b**) from an arable area to a forest. In both cases, soil biodiversity increases and the soil releases less CO_2 into the atmosphere. (WIP, TFO)

Regulating services – Atmospheric composition and climate regulation

Nutrient cycles

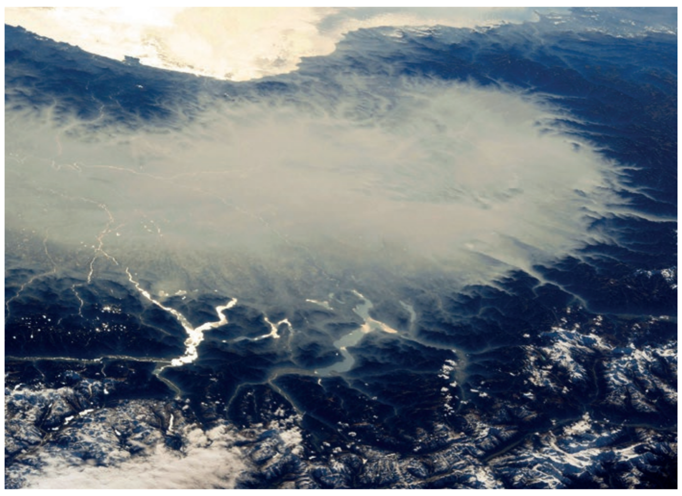
Nutrient cycling is the transformation of nutrients contained in minerals from the original bedrock and in dead biomass into forms that are assimilable by plants and other organisms. In this way, nutrients can enter the cycles that will transfer them from the biosphere to soil, water and the atmosphere. The main nutrients are carbon, nitrogen and phosphorus. All soil organisms contribute to this major ecosystem function through a number of physical (e.g. bioturbation and transport of soil particles) and chemical (digestion by a large number of enzymes) processes. [131]



Soil organic carbon map based on a reclassification of the FAO-UNESCO Soil Map of the World combined with a soil climate map. The map shows the global distribution of soil organic carbon to a depth of one metre (derived from USDA Natural Resources Conservation Service). (LJ, JRC) [133]

Carbon cycle

The transfer of carbon (C), in its many forms, between the atmosphere, living organisms (biosphere), oceans and soils (pedosphere) is described as the carbon cycle. In the atmosphere, carbon can be found in two main forms: carbon dioxide and methane (see page 102). Carbon dioxide (CO_2) moves from the atmosphere to the terrestrial biosphere through photosynthesis (see box on page 35). Photosynthesis is a process used by plants and other organisms (such as bacteria – see pages 33-35) to convert light energy and CO_2 into chemical energy, in the form of carbohydrates (sugars). Carbon leaves the terrestrial biosphere in several ways, including through the combustion of fossil fuels and metabolic respiration by plant and soil organisms. Human activities have modified the carbon cycle by directly adding carbon to the atmosphere (e.g. through industrial activities).



Human activities impact carbon cycling by increasing the releases of CO_2 into the atmosphere, as clearly visible in this photograph from space. This leads to an unbalanced C cycle, with emissions higher than the fluxes returning to Earth. (SRN)

Unbalanced budget

Currently, the global carbon budget is unbalanced, meaning that the release of CO_2 into the atmosphere is higher than fluxes into carbon sinks, such as peat and some tropical soils. This unbalance is caused by direct human activities.

It is estimated that ~215 Gt (gigatonne = 10^{12} kg) of carbon are removed from the atmosphere annually through photosynthesis (~123 Gt) and absorption by the oceans (~92 Gt). Total annual emissions amount to an estimated ~219 Gt via the auto- (~60 Gt) and heterotrophic (~60 Gt) respiration (see page 30) of terrestrial systems and releases from the oceans into the atmosphere (~90 Gt). In addition, anthropogenic activities, primarily through the use of fossil fuels, account for ~9 Gt C per year.

Although this may seem to be a small contribution, it has significant consequences as it creates an imbalance in the global carbon cycle, converting the Earth from a net C sink of ~2 Gt per year to a net source of ~4 Gt per year. Increased use of fossil fuels for industrial activities has led to the release of carbon, previously stored in the Earth for millennia, into the atmosphere. Simultaneously, reductions in forested areas (due to conversion into agricultural land or urbanisation) have created a significant reduction in the global C sink, since forests are one of the main terrestrial sinks for atmospheric CO_2. The main consequences of this imbalanced C budget are the potential interactions with and feedbacks of climate change.

Soil biodiversity and the carbon cycle

Soils are of considerable importance for carbon cycling in terrestrial ecosystems, as a large proportion of the global terrestrial C pool (approximately 80%) is stored underground. Furthermore, soils represent the main habitat for organic matter decomposition (see page 106). Consequently, the flux of belowground C to the atmosphere through respiration and decomposition is rather substantial. Of the total soil respiration, heterotrophic soil biota account for around half, while the remainder is respired by plant roots (see page 43) and associated mycorrhizal fungi (see page 40).

Soil respiration chambers are used to measure CO_2 emissions by soil organisms. (ORNL)

Soil species richness allows for myriad interactions, many of which alter aspects of C cycling. Soil microbes (e.g. bacteria and fungi – see pages 33-35, 38-41) are responsible for the vast majority of respiration and decomposition in soils.

However, the presence of soil fauna (see Chapter II) greatly stimulates rates of respiration and decomposition, despite the relatively minor direct contribution of animals to these processes. The positive impact of soil fauna on C cycles has been attributed to: 1) litter fragmentation, which increases the surface area available for colonisation by microbes; 2) partial digestion of litter, which often enhances decomposability; 3) bringing microbes and organic matter into direct contact with each other; for example, earthworms dragging leaf litter from the soil surface into the soil matrix; and 4) grazing on the microbial community, which can stimulate their activity.

Organic versus inorganic

- In chemistry, molecules can be referred to as being organic or inorganic. The primary difference is that organic compounds always contain carbon, while most inorganic compounds do not.
- Almost all organic compounds contain carbon-hydrogen bonds. Only a few organic compounds do not contain carbon-hydrogen bonds (e.g. carbon tetrachloride – CCl_4).
- Molecules associated with living organisms are organic. These include nucleic acids, fats, sugars and proteins. For example, the sugar glucose ($C_6H_{12}O_6$) is organic.
- Inorganic molecules include salts, metals and substances made of single elements. For example, calcium carbonate ($CaCO_3$) is inorganic.

It is reasonable to suppose that shifts in soil species richness and composition could influence C cycling through changes in the interactions among soil biota. Because of the complexity of soil life, the relationships between species richness, composition and C cycling vary substantially, from positive (i.e. increasing the process rate) to negative. Studies have demonstrated that species richness is mainly of importance to C dynamics in soils with low species richness. Due to the potential functional redundancy (see page 97) in soil communities, changes in composition are of greatest importance for C dynamics. Therefore, if a community is dominated by one species and subjected to selective stress that reduces its abundance, the impact on the C cycle will be greater. In conclusion, while the direct effect of altered species richness resulting from global change may have comparatively small effects on the C cycle, changes in the abundance of species within a soil community may alter C cycling quite significantly.

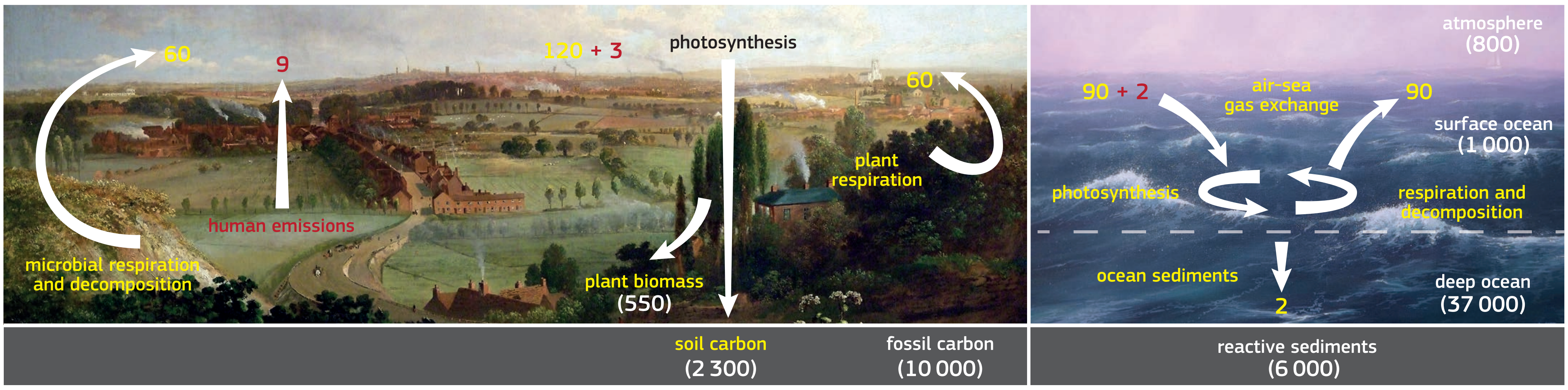


Diagram of the rapid carbon cycle, showing the movement of carbon between land, atmosphere and the oceans. The yellow numbers represent natural fluxes, whereas the red ones represent human contributions, both in gigatonnes of carbon per year. The white numbers indicate stored carbon (adapted from US DOE, Biological and Environmental Research Information System). (FUT, AMA, JRC) [132]

Nitrogen cycle

The nitrogen cycle is the process by which nitrogen (N) is converted into its various chemical forms. Nitrogen is necessary for all known forms of life on Earth to produce proteins. As such, the nitrogen cycle is an important part of every ecosystem. A large portion of the nitrogen cycle takes place in the soil. The main nitrogen inputs to the soil are made through:

- biological fixation
- industrial fixation (i.e. commercial fertilisers)
- soil organic matter
- rain (deposition of industrial emissions)
- crop residues and animal manure

Nitrogen, already present in or added to the soil, is subjected to several transformations that dictate its availability to plants. Nitrogen is present in the environment in a wide variety of chemical forms, including organic nitrogen, ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), nitrous oxide (N_2O – see page 103), nitric oxide (NO) and inorganic nitrogen gas (N_2). The main processes of the nitrogen cycle that transform nitrogen from one form to another are the following:

- nitrogen fixation is the process whereby atmospheric nitrogen is converted into ammonium
- ammonification or mineralisation is the conversion of organic nitrogen into ammonium
- nitrification is the conversion of ammonia into nitrates
- assimilation is the uptake of nitrogen from the soil by plants, in the form of either nitrate ions or nitrite ions
- denitrification is the reduction of nitrates back into nitrogen gas

Nitrogen cycle and soil biodiversity

Chemical engineers (see box on page 95) play a key role in the soil nitrogen cycle. Firstly, bacteria or fungi convert the organic nitrogen from decaying animals or plants into ammonium (NH_4^+). A number of microorganisms (e.g. bacteria and fungi) are able to perform this first ammonification step. In N-limited ecosystems, such as the Arctic and Alpine regions (see pages 84-85), some microbes may directly use organic nitrogen forms, such as amino acids, thereby bypassing this mineralisation step.

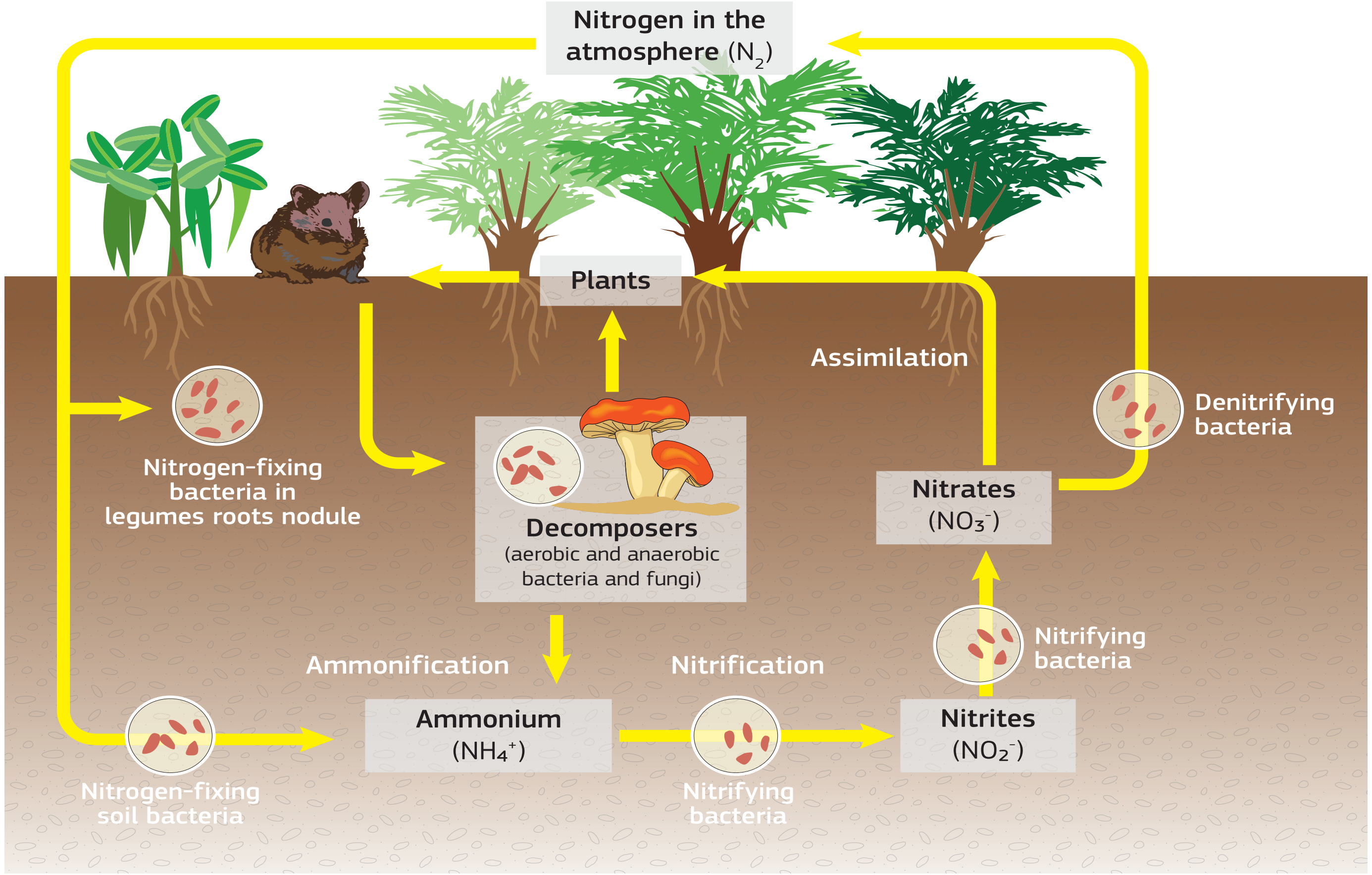
After ammonification, the chemical processes are carried out by specialist groups of bacteria. The nitrification process is carried out by bacteria called ammonia-oxidising bacteria (AOB), which convert ammonia into nitrites (NO_2^-) that are toxic to plants. Other groups of bacteria oxidise nitrites into harmless nitrates (NO_3^-) that are useful for plant growth. Nitrification processes are also carried out by groups of archaea (see page 32) called ammonia-oxidising archaea (AOA). Ammonium can also be directly produced from atmospheric nitrogen by nitrogen-fixing bacteria. Some of these microorganisms are free-living in the soil (e.g. bacteria of the genus *Azotobacter*), whereas species of *Rhizobium* (see page 34) live in a symbiotic association with leguminous plants (see page 99).

Plants can absorb ammonium or nitrate from the soil via their root hairs, or through symbiotic relationships with rhizobium bacteria. For the nitrates that are not absorbed by plants, denitrification can take place. This process, which converts nitrate into atmospheric nitrogen, is performed by certain bacteria in anaerobic conditions. These bacteria do not require air, but rather use nitrogen instead of oxygen.

Soil engineers (see box on page 95), such as earthworms and termites (see pages 55, 58), also influence the N cycle. Due to the increased nutrient availability, their structures (e.g. earthworm casts and burrows) are rich in microbial diversity and become preferred sites for a number of soil processes, such as nitrogen fixation. In conclusion, all the described steps clearly show the role played by soil biodiversity in regulating the nitrogen cycle and, consequently, other ecosystem services related to it, especially plant growth support (see pages 98-99).

Phosphorus cycle and soil biodiversity

The phosphorus (P) cycle describes the movement of phosphorus through the soil, water and living organisms. The atmosphere does not play a significant role in this cycle. Phosphorus is an essential nutrient for all organisms since it is incorporated into many molecules that are essential for life, such as DNA (see box on page 30).



Schematic representation of the main flows of nitrogen (N) through the terrestrial environment. The importance of soil bacteria and fungi in the cycle is immediately recognised as being a key element, providing different forms of N compounds assimilable by higher organisms, such as plants. (JJB, FVI, NLA, NRCS)

For example, studies have shown that P is the limiting nutrient for plant growth. Phosphorus enters the environment from ancient rocks or deposits and is, similar to soil itself, a non-renewable resource.

Phosphorus occurs in both organic and inorganic forms (see box on page 104). Soil P chemistry is very complex, with more than 200 possible forms of P compounds being affected by a variety of biological, physical and chemical factors. The relative amounts of each form of phosphorus vary greatly among soils, with the total amount of P in a clayey soil being up to ten times greater than in a sandy soil (see Chapter I).

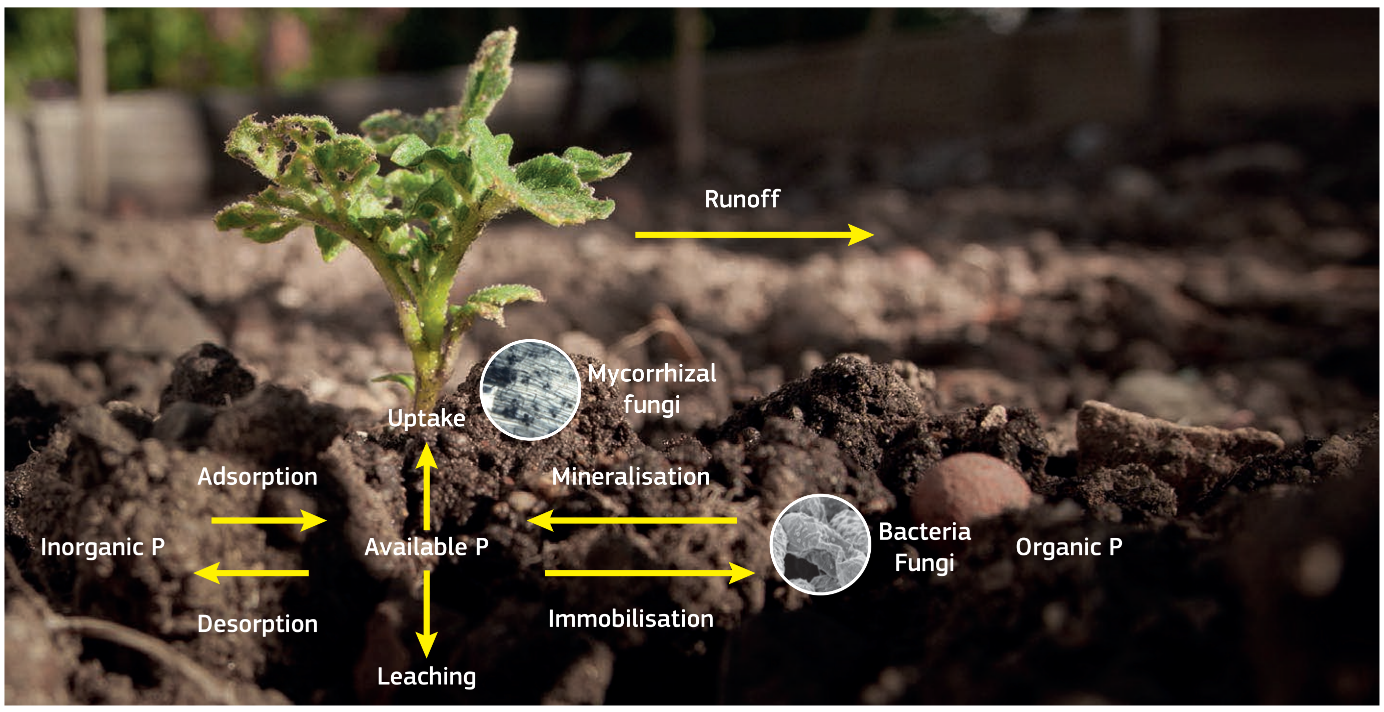
Soil organic P comprises many different compounds, the majority of which are of microbial origin. Organic P is locked up in the soil and is generally not available for plant uptake until the organic materials are decomposed and the phosphorus released via the mineralisation process. Mineralisation is carried out by soil microorganisms (e.g. bacteria) and, similar to nitrogen, the rate of P release is affected by abiotic factors, such as soil moisture, composition of organic material, oxygen concentration and pH. For example, P availability to plants in most soils is greatest when the soil pH is in the range of 6 to 7. The reverse process to mineralisation, known as immobilisation, refers to the tie-up of P by microbes that use it for their own nutritional needs. Microorganisms may compete with plants for P when concentrations are low. However, the roots of many plant species enter into symbiosis (see box on page 33) with mycorrhizal fungi (see page 40), which promote the acquisition of phosphorus.

Mineralisation and immobilisation occur simultaneously in the soil. If the P content is high enough to fulfil the requirements of the microbial population, mineralisation will be the dominant process.

Soil phosphorus losses to the environment through runoff and/or leaching may create agricultural issues. Insufficient soil P can result in delayed crop maturity, reduced flower development, low seed quality and decreased crop yield. Runoff is a result of soil-bound P being carried away by water (soil erosion). Leaching is the removal of P from the soil by the movement of vertical water. Microbial mineralisation allows the slow release of P into the soil during the growing season, thus making it available for plant uptake. This process reduces the need for fertiliser applications as well as the risk of runoff and leaching.

The inorganic P content is regulated by other mechanisms. Adsorption is the chemical binding of P to soil particles, which makes it unavailable to plants. Desorption is the release of adsorbed P from its bound state into the soil solution, where it becomes accessible to roots.

The P cycle is also indirectly regulated by soil organisms other than microbes, sucha as protists (see pages 36-37) and nematodes (see pages 46-47) that feed on bacteria and fungi responsible for the mineralisation processes. It has been shown that the elimination of nematodes reduces nutrient mineralisation and consequently causes a decrease in phosphorus uptake by plants.



Simplified phosphorus (P) cycle in the soil. The regulation of soil P cycling is influenced by microorganisms (e.g. bacteria and fungi). (DG, JRC)

Regulating services – Atmospheric composition and climate regulation

Decomposition

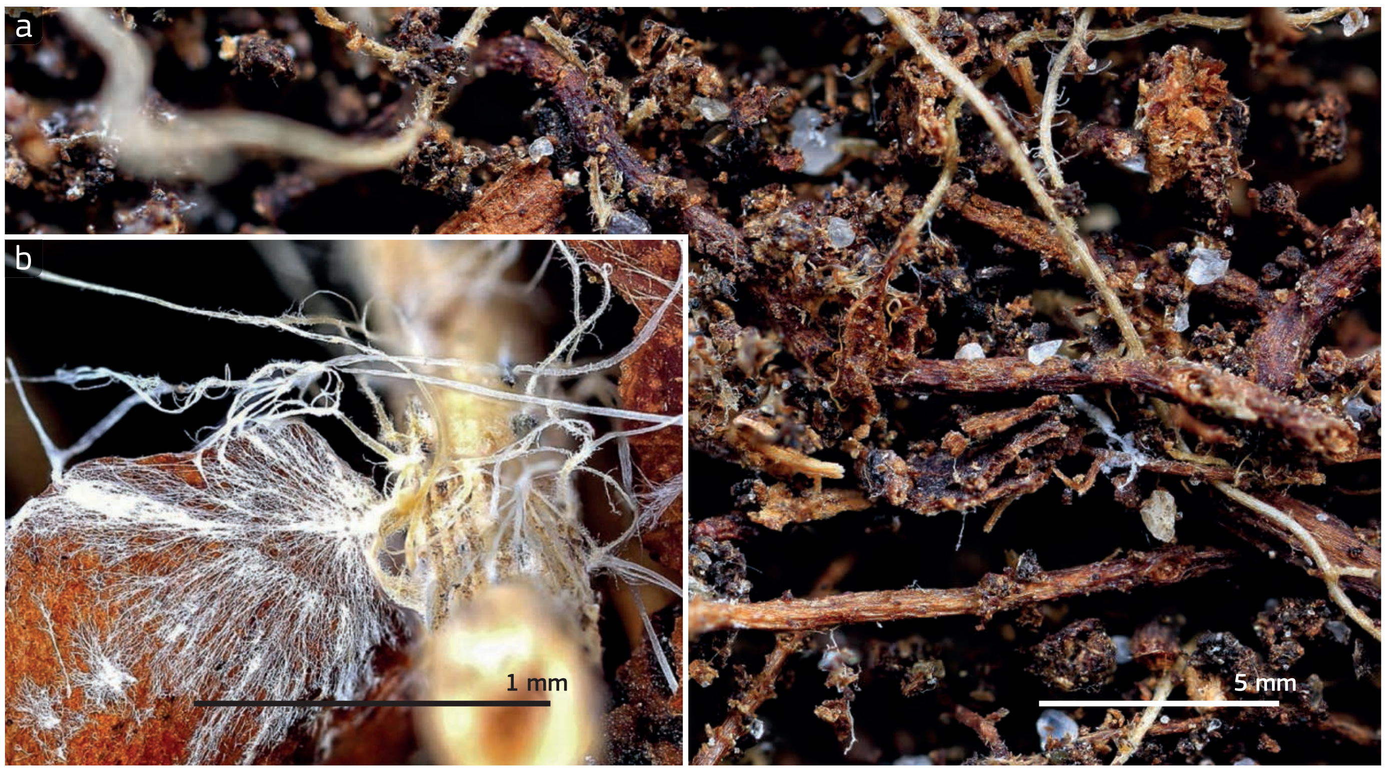
In a continuous cycle of life and death, plants, flowers and animals live and die. What remains is either broken down by a huge array of microorganisms (e.g. bacteria and fungi – see pages 33-35, 38-41) already living belowground or carried there by invertebrates, such as isopods, earthworms or beetles (see pages 56, 58-59), where it continues to break down. The reduction of raw organic materials to a compost is known as decomposition and results in the production of soil organic matter (SOM). In fact, SOM can be defined as the organic component of soil, consisting of plant and animal residues at various stages of decomposition. Nutrients that are created from the decomposition processes are dissolved when water is added to the soil, providing plant roots with a constant supply of nourishment over time. Decomposition processes also generate long-term SOM and play an important role in the global nutrient cycles. [134]

Litter decomposition is the initial phase of humus formation. It occurs at a very variable rate depending on the soil properties (e.g. temperature and pH) and the nature of the plant residues forming the litter. (DST)

The prime source of SOM is plant debris of all types, such as dead leaves and branches, that fall onto the soil and are then decomposed at varying rates depending on their composition. Organic compound degradation is ranked, in descending order, as follows:

1. sugars and starches
2. proteins
3. hemicelluloses
4. cellulose
5. lignins and fats

Plant residues containing these compounds form the fresh organic matter that is converted into a more stable and resistant form known as 'humus', through decomposition processes, also known as 'humification'.



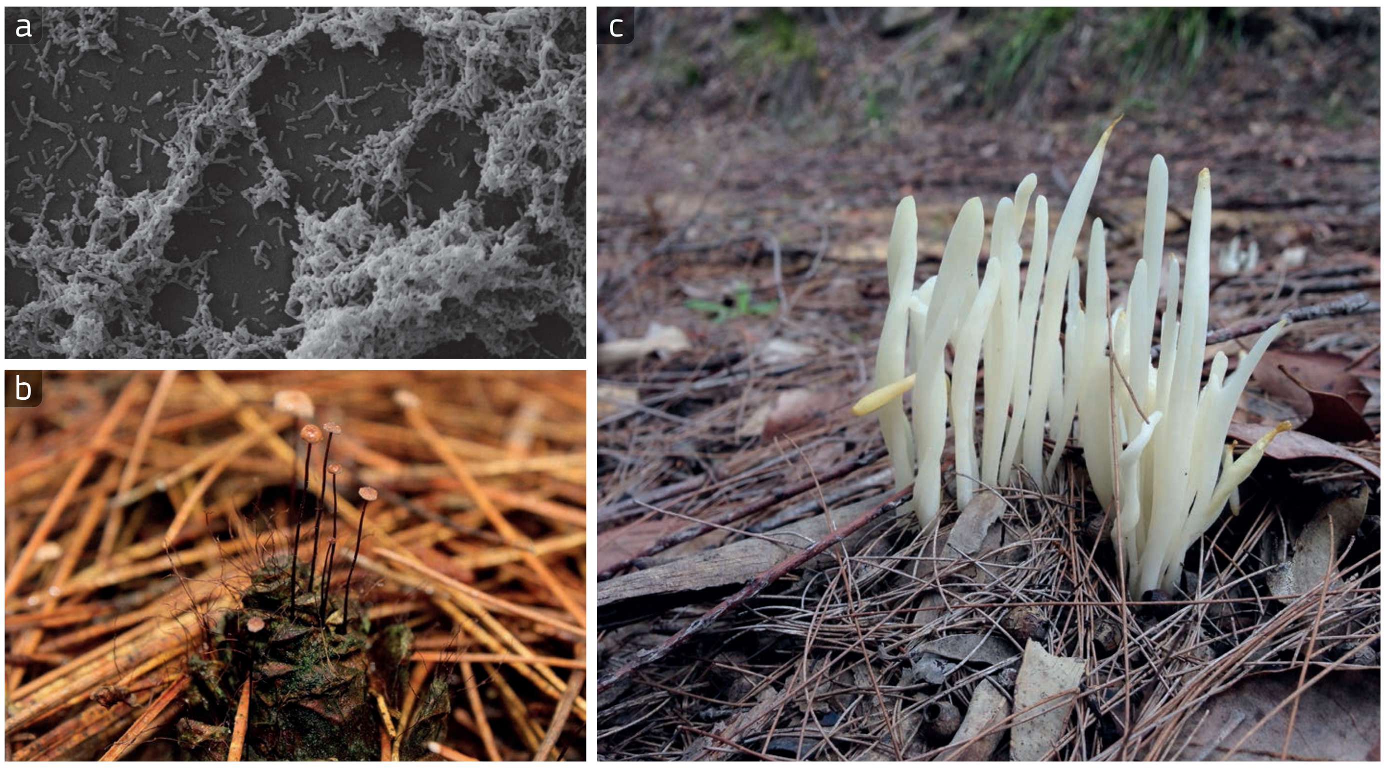
(**a**) A close-up view of the litter layer in which soil microorganisms, namely fungi and bacteria, decompose organic matter. (**b**) An even closer view of a fungus with its white mycelium (see box on page 39) surrounding a leaf. Fungi take nutrients from plant residues by decomposing them. (CDH, YKN)

Decomposition of organic matter in soils is accomplished largely by microorganisms, often in association with invertebrates. Soil microbes, the chemical engineers (see box on page 95), have the appropriate enzymes to break down complex molecules (e.g. lignin) present in plant debris. Soil invertebrates accelerate decomposition in several ways: 1) arthropods (see Chapter II) carry plant matter below the soil surface, where it is prevented from being removed by wind or water and stays moist longer, resulting in more rapid decomposition; 2) organic matter can be ingested, digested and excreted (e.g. by earthworms); 3) organic matter is shredded into smaller pieces, giving fungi and bacteria more surface area for attack; 4) they create macropores, or soil cavities, that allow more water to enter the soil, thus extending activity times for the decomposers, as most are only active in moist environments.

Types of humus

- There are three main types of humus: Mor, Moder and Mull.
- Mor humus is a thick mat of undecomposed to partially decomposed litter, typical of coniferous forests.
- Moder humus is formed by undecomposed and partially decomposed remains of broad-leaved deciduous forest litter.
- Mull humus is well-decomposed organic matter, produced in very biologically active habitats.

Since the decomposition process is carried out by living organisms, it is affected by several environmental variables, including soil moisture, temperature and pH.



Soil (**a**) bacteria and (**b–c**) fungi play a key role in decomposition processes as they contain the enzymes needed to degrade complex compounds present in plant residues. (TPF, LD, DBE)

For example, cold and acidic soils, such as those of peatlands and boreal forests (see page 79), have low microbial activities and low invertebrate diversity, which means that plant material is decomposed slowly. In tropical forests (see page 78), the whole process is much more rapid because moist conditions and high temperatures enhance biological activity. Finally, decomposition processes are affected by the type of residues and, in particular, by their carbon-to-nitrogen (C:N) ratio.

Carbon-to-nitrogen ratio

The carbon-to-nitrogen ratio represents the relative proportion of the two elements present in a substance. For example, a material containing 30 times more carbon than nitrogen is said to have a C:N ratio of 30:1. The C:N ratio of the organic material influences its decomposition. Indeed, organisms that decompose organic matter use carbon as a source of energy and nitrogen for building cell structures (e.g. proteins).

In the soil, organic matter with excess carbon can create problems. To continue decomposition, the microbial cells use any available soil nitrogen, for which they have to compete with plants. This is known as 'robbing' the soil of nitrogen, and reduces the availability of nitrogen as a fertiliser for plant growth. So, if there is too much carbon, decomposition slows and plant growth may be problematic. Conversely, when the energy source (i.e. carbon) is less than that required for converting available nitrogen into proteins, decomposition is faster and organisms make full use of the available carbon and get rid of the excess nitrogen as in the form of ammonia released into the atmosphere (see page 105). This also can also be an issue as it results in losses of nitrogen from the soil.

Since organisms use about 30 parts carbon for each part nitrogen, an initial C:N ratio ranging from 20 to 30 promotes rapid composting. Examples of C:N ratios in organic material are:

- food scraps: 15:1
- grass clippings: 19:1
- oak leaves: 26:1
- leaves: from 35:1 to 85:1
- maize stalks: 60:1
- straw: 80:1
- pine needles: from 60:1 to 110:1
- farm manure: 90:1
- alder sawdust: 134:1
- newspaper: 170:1
- Douglas fir (*Pseudotsuga menziesii*) bark: 490:1

In conclusion, all soil organisms, from bacteria to the largest of the invertebrates, are part of complex interactions that lead to the decomposition of organic matter. As decomposition is the main process that recycles nutrients (e.g. carbon and nitrogen) back into the soil, soil biota is crucial to nutrient cycles and, consequently, to the regulation of the atmospheric composition and climate.

Regulating services – Water supply and quality

Water supply

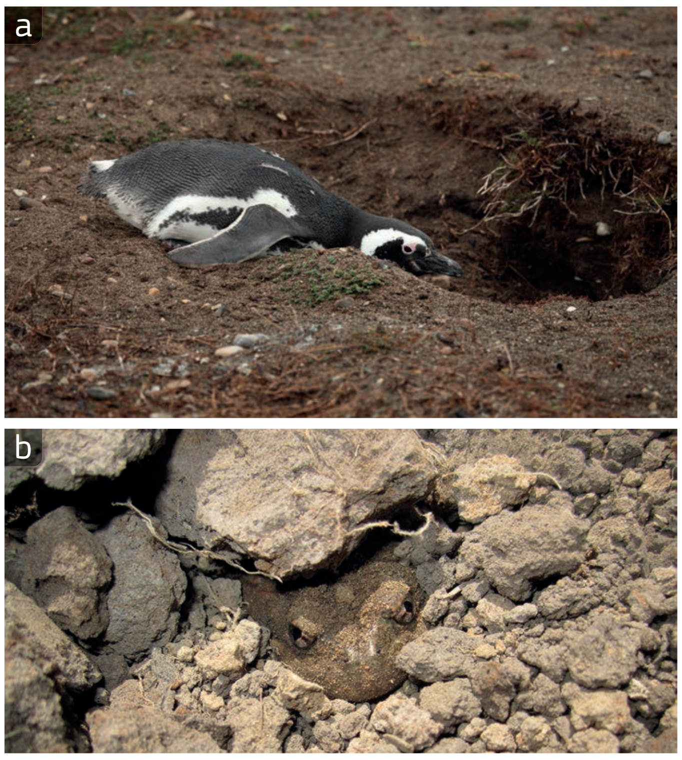
The safeguarding of soil hydrological services relies strongly on the activity of soil biota. Their role in maintaining soil structure, has both direct and indirect implications for water supply and water quality regulation. In particular, those organisms contributing to the formation of macropores and tunnels have a direct effect on water, air and nutrient movement through soil profiles. They include all the burrowing soil creatures, such as earthworms, social insects and their larvae (see page 54-55, 58, 60), as well as some vertebrate groups, such as moles, rabbits, foxes and badgers (see page 62-63). [135]

Some numbers may explain the ability of soil organisms to dig soil. For example, some earthworm species in Tasmania dig burrow with diameters that range from < 1 mm to > 10 mm, and depths of up to 15 m. Furthermore, it has been conservatively estimated that earthworms can dig about 17 - 40 tonnes of soil per hectare per year. Just one tropical species, *Eudrilus eugeniae* (the 'African Night Crawler'), produces around 157 tonnes per hectare of surface casts per year. With regard to ants, there is a general trend of increasing subterranean tunnel networks with increasing colony size. For example, one of the largest colonies ever found was in Japan, containing over 300 million worker ants and one million queens living in 45 000 nests interconnected by underground passages over an area of 2.7 km^2.

A cross-section of an ant nest shows the parts of tunnels where water can easily infiltrate. (AOI)

The European mole (*Talpa europea*) continuously searches for food, running through its network of tunnels, which can often reach lengths of over 70 m and can vary in depth from just under the surface to up to 70 cm deep. The Zambian mole-rat (*Fukomys amatus*) digs some of the longest tunnels in the natural world. A single underground colony, containing just ten mole-rats, can stretch for 2.8 kilometres. Another great digger is the badger. Its tunnels can have a combined length of several hundred metres, although individual tunnels rarely exceed 15 metres in length. All these numbers clearly show the positive impact of soil-living organisms on water circulation in the soil.

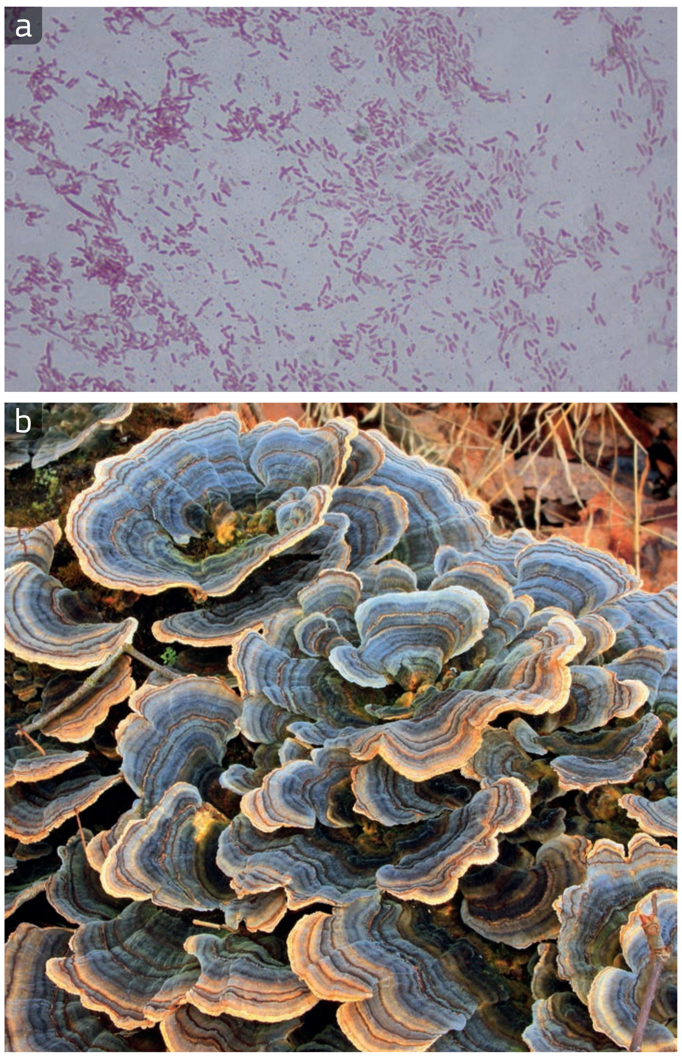
(**a**) European badgers (*Meles meles*) are often unpopular because they alter the landscape through (**b**) burrows that they use as 'badger setts'. However, these structures allow water and air to move within the soil. (JGO, FUT)



Soil water supply may also be guaranteed by larger animals, such as (**a**) the Magellanic penguin (*Spheniscus magellanicus*) and (**b**) toads, which are not properly considered as soil biodiversity, but rather soil-nesting organisms. (LQU, POR)

Water quality

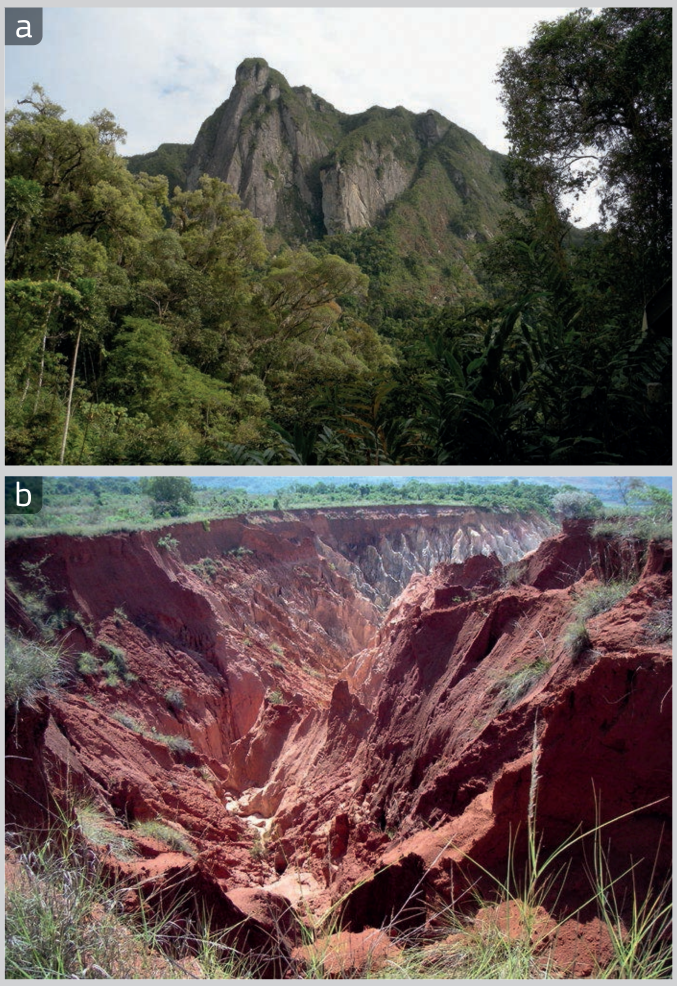
Soil detoxification and water 'filtration' are essential for maintaining the quality of soil and, consequently, that of our surface and groundwater resources. Soil water purification is carried out abiotically (e.g. interactions with organic and inorganic soil particles) and biotically (through adhesion, binding and adsorption onto microbial cells and soil organisms), with any potential soil contaminants also being subjected to dispersal through bioturbation and burrowing activities. In addition to these physical processes, biotransformation and degradation of xenobiotic compounds and contaminants (e.g. metals, pesticides and solvents) within the soil also take place in natural environments, carried out mainly by native heterotrophic (i.e. carbon-eating) soil bacteria (e.g. genus *Pseudomonas*, *Micrococcus*, *Streptomyces*, *Corynebacterium* and *Thiobacillus* – see page 33-35) and most wood-degrading fungi (e.g. white-rots, such as *Phanerochaete chrysosporium* and *Trametes versicolour* – see page 38-41, 100).

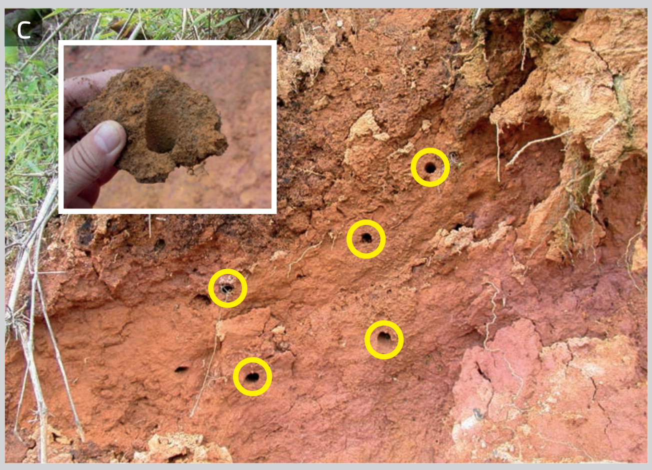


(**a**) Cells belonging to the bacterial genus *Pseudomonas* and (**b**) the wood-degrading fungus *Trametes versicolour*. These organisms are able to remove toxic compounds from soil and water, thus allowing for the maintenance of good soil quality. (RIR, NAT)

Hydraulic engineers in Malagasy rainforests

- In the southeastern part of Madagascar, very fragile soils are protected from erosion by structures created by soil ecosystem engineers (i.e. arthropods in the litter layer and earthworms in the mineral horizon). [136]
- Rainforests grow on very deep soils that are highly prone to erosion due to their specific composition and structure.
- The soil is protected by a 10 - 15 cm thick humic horizon mainly comprised of arthropod (especially dipteral larvae) faecal pellets that are greatly hydrophilic. This layer can absorb between 20 and 100 mm rainfall, thus preventing surface runoff and subsequent surface erosion.
- Below this humic layer that acts as a sponge, the mineral soil exhibits subhorizontal earthworm galleries that form a network of tubular voids that are regularly spaced and with similar diameters. These galleries connected to the surface by vertical sections likely allow for drainage of water from the surface layer to deeper soil layers and to aquifers.
- Deforestation and the consequent elimination of the ecosystem engineers that maintain these structures trigger soil erosion.





Rainfall and massive deforestation of (**a**) tropical rainforest led to erosion events. (**b**) Lavaka, the Malagasy word for 'hole', usually found on the side of a hill, is a type of erosional feature common in Madagascar. (**c**) Earthworm burrows allow water to flow away, thereby reducing the erosion risk. (FVA, PL)

Regulating services – Biological population control

Soils are also home to organisms that can cause disease in animals, humans and plants. It should be stressed, however, that the vast majority of organisms found in the soil do not cause diseases but rather provide a myriad of ecosystem services that are vital for the maintenance of life on Earth, including the regulation of pathogens and pests. Furthermore, disease-causing organisms are often not efficient competitors in the soil and, as such, increased soil biodiversity is usually correlated with reduced numbers of disease-causing organisms. Here we discuss some of the organisms found in the soil that can cause diseases in humans, livestock and crops. We also present the ability of the soil biota to regulate the spread and incidence of pathogens and pests. [137]

Human and animal diseases

There is considerable overlap between human and animal diseases caused by soil organisms – after all, humans belong to the animal kingdom. There are a few notable exceptions, which are discussed in more detail below. There is no general consensus on what constitutes a soil-borne disease, but in a report published by the European Commission, soil-borne diseases are defined as:

'...resulting from any pathogen or parasite, transmission of which can occur from the soil, even in the absence of other infectious individuals'.

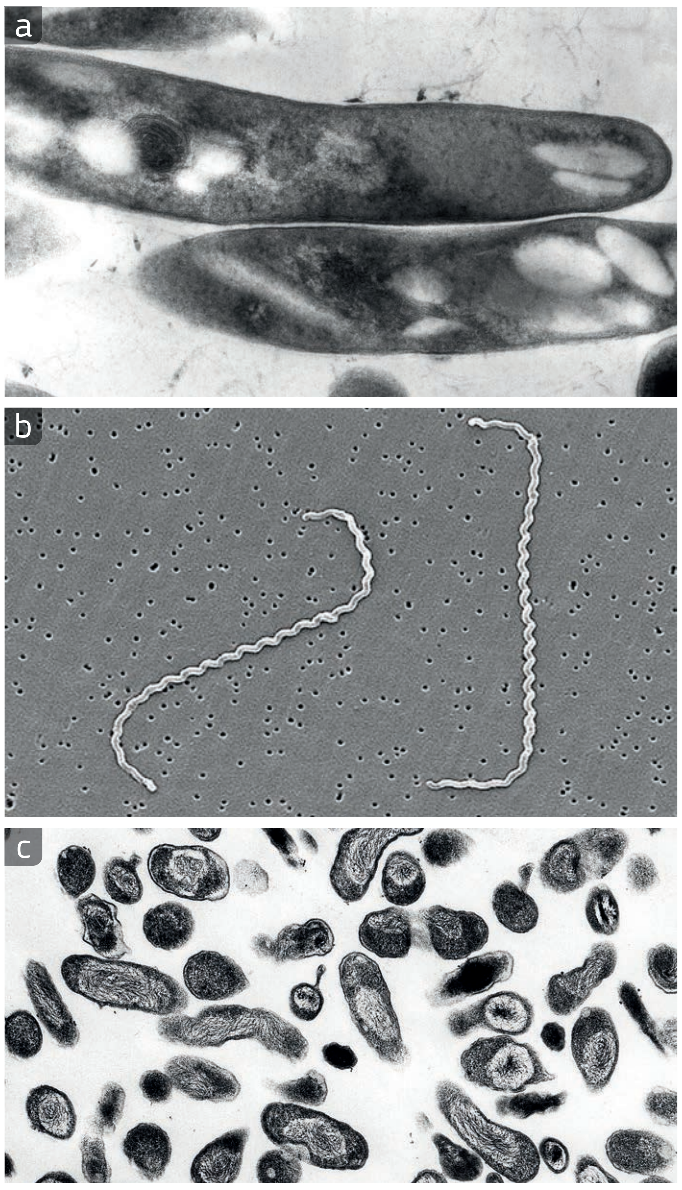
It is important to note that the disease can be spread even in the absence of infectious individuals. Many diseases could be passed through the soil in quite contrived circumstances. For example, many viruses can only survive on the soil surface for a very short period of time. It is unlikely that such diseases would infect a new host if the infectious individual is no longer present – transmission through the air when in close contact with an infected person is much more likely. If all such diseases were included, it could potentially 'cloud the water' in terms of identifying soil-borne diseases and potential mechanisms by which their incidence may be reduced.

Euedaphic pathogenic organisms and soil-transmitted pathogens

Human and animal pathogens and parasites can be divided into two groups. Euedaphic pathogenic organisms (EPO), which are true soil organisms (i.e. their usual habitat is the soil and they are able to complete their lifecycles in the soil without infecting a host). These include most of the bacterial pathogens and all of the fungal pathogens, some of which have important implications for human health. For example, *Clostridium tetani* is an EPO with a worldwide distribution in soil and is the causative agent of tetanus. In 2006, 290 000 people died of tetanus, of which 250 000 were neonatal deaths.

Tetanus, caused by the soil bacterium *Clostridium tetani*, still causes many deaths among unvaccinated children. (HDP)

The other group consists of soil-transmitted pathogens (STP). These organisms must infect a host in order to complete their lifecycles, but are able to survive for extended periods of time in the soil. This group includes viruses and parasites. The utility of such a distinction is that EPO are likely to provide or contribute toward ecosystem services provided by the soil biota. For example, many of the disease-causing fungi (which are EPO) are hyphal and play an important role in soil structure maintenance, as well as in stabilising the soil surface by binding soil aggregates together. In deserts (see page 87), for example, which have low species richness, removal of disease-causing fungi, through the application of fungicide, may have a negative impact on soil surface stability, leading to an increase in the risk of soil erosion.



The soil-borne pathogen (**a**) *Mycobacterium tuberculosis* causes tuberculosis while (**b**) bacteria of the genus *Leptospira* is the causative agent of Leptospirosis and (**c**) *Coxiella burnetii* is the causative agent of Q fever. (CDC)

STP will often be in a dormant form within the soil and are likely to contribute much less to the provision of ecosystem services. As such, treatments or land management practices that reduce the numbers of such organisms within the soil are likely to have much more limited impacts on the provision of ecosystem services.

Domestic animal diseases

Soil-borne pathogens may also affect domestic animals, such as livestock, whith both economic and health implications. The most direct economic impacts of livestock diseases are loss of production and/or productivity, and the cost of treatments. Estimates of the economic costs to agriculture of the outbreak of foot-and-mouth disease in the United Kingdom suggest a loss of approximately 20 % of the total income from farming in 2001. The causative agents of bovine spongiform encephalopathy (BSE, commonly known as mad cow disease), the severe acute respiratory syndrome (SARS) and avian influenza (H5N1 and H1N1) can survive for extended periods of time in the soil. These diseases are estimated to have caused over US$20 thousand million (approx. €19 bn) of direct economic losses over the past decade and much more than US$200 thousand million (approx. €186 bn) in indirect losses.

From a human health perspective, zoonotic diseases (passed from animals to humans) represent the majority of infectious diseases that have the potential to become pandemic. However, it should be noted that the majority of zoonotic diseases are not soil-borne, or at most are STP. Of the 1 415 known human pathogens, 62 % are of animal origin. On average, a new disease has emerged or re-emerged each year since the Second World War, and 75 % of these were zoonotic. The influenza pandemic that killed 50 - 100 million people between 1918 and 1919 had largely faded from public memory by the late 1990s and early 2000s, when outbreaks of SARS and avian influenza occurred. Other examples of soil-borne zoonotic diseases include: anthrax, giardiasis, leptospirosis, Q fever and tuberculosis.

Plant diseases

Plants are the key primary producers in most terrestrial ecosystems and generally exploit soils for resources, using complex root systems.

The root exudates allow for the maintenance of a dynamic and nutrient-rich niche around the root-soil interface called the rhizosphere. The diversity of nutrients and plant secondary metabolites present in the exudates allows for the enrichment of specific taxonomic or functional groups of microbes in the rhizosphere. Soil microbes interact with plant tissues and cells with different degrees of dependence, and have developed several strategies for adapting to the plant environment.

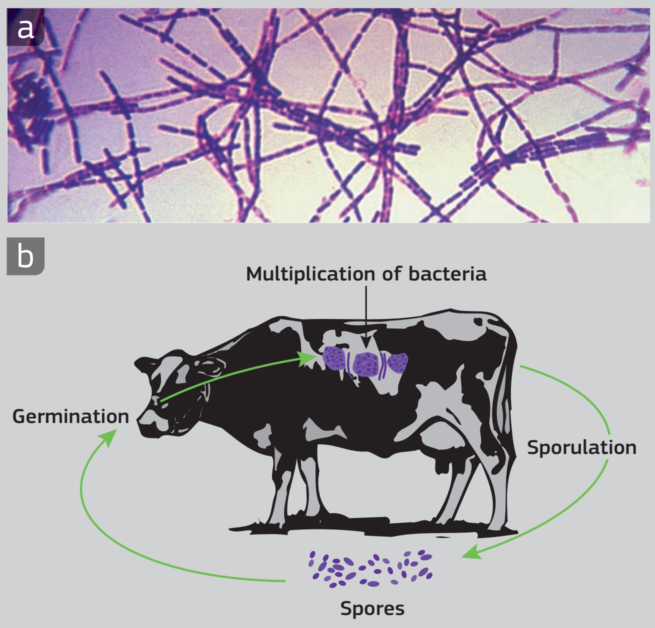
Plant-microbe interactions include competition, commensalism, mutualism, and parasitism (see box on page 33). However, because of its enormous economic importance, one aspect of plant-microbe interactions that has been extensively studied is the plant-pathogen interaction. Losses caused by soil-borne plant pathogens remain important constraints on efforts to increase plant production and productivity worldwide.

Plant diseases are mainly caused by fungi, viruses, bacteria, nematodes and protists. Among fungi, disease-causing organisms mainly belong to the Ascomycota and Basidiomycota groups (see pages 38-39). *Fusarium* spp., *Verticillium* spp., *Ustilago* spp. and *Puccinia* spp. are well known plant disease causal agents. Among protists (see pages 36-37), *Phythium* spp. and *Phytophthora* spp. are also known for their infectivity. Bacterial disease, by comparison, is less severe and inflicts less economic damage. Most of plant pathogenic bacteria belong to the Actinobacteria and Proteobacteria phyla (see pages 33-35). The most common plant pathogenic bacteria include *Agrobacterium* spp., *Erwinina* spp., *Xanthomonas* spp. and *Pseudomonas* spp. Similarly, some nematodes (e.g *Globodera* spp. and *Meloidogyne* spp. – see pages 46-47) parasitise crop roots and cause significant crop loss in the tropics and subtropics.

The severity of damages and economic costs can be minimised through the use of agrochemicals to control disease-causing organisms, by selecting cultivars that are resistant to particular diseases or using agronomic practices (e.g. crop rotations, seed treatments).

Anthrax and soil

- *Bacillus anthracis* is the name of the causative bacterium of the disease anthrax.
- Despite perhaps being more infamous for its potential use as a bio-warfare agent, the bacteria is actually a relatively common disease of wild and domestic animals, as well as livestock, causing approximately one death per million animals at risk.
- Cases have been declining since the second half of the 20th century due to control and prevention programmes, including measures, such as vaccination, being introduced.
- It can, very occasionally, infect humans but it seems that birds have a natural resistance to anthrax disease.
- The bacterium itself is highly robust and able to dehydrate itself to form a resistant spore that allows it to survive on, for example, times of drought.
- In this state, the organism is also resistant to high temperatures, freezing cold and many disinfectants. The organism thrives particularly well in alkaline soils and is able to grow when conditions, such as moisture, temperature and access to nutrients, are favourable.



(**a**) Photomicrograph of *Bacillus anthracis*, the cause of the anthrax disease. (**b**) Simplified anthrax lifecycle. The disease affects almost any animal, but those most susceptible are large herbivores, such as cows. The bacterium responsible for this disease can survive as spores in the soil for extended periods of time. (CDC, JRC)

Pest and pathogen regulation

Pests and pathogens are regulated or maintained below harmful levels by a specific combination of:

a. biotic factors, such as predators, pathogens, competitors and hosts
b. abiotic factors, such as climate and land use (agricultural or urban)
c. socio-economic factors, such as disease or pest management

The relative role of abiotic, biotic, and socioeconomic factors in regulating specific pathogens and pest systems is largely unknown. Considering the biotic factors, different components of biodiversity may be involved in the regulation processes. Analyses have shown that, on average, increasing the diversity of natural enemies (i.e. predators, parasites and pathogens) generally strengthens pest suppression. Therefore, it is possible to biologically control pests by means of other organisms. Biocontrol can be obtained through three main strategies: conservation, augmentation or importation of natural enemies.

Conservation is based on the preservation of existing natural enemies by choosing cultural, mechanical or selective chemical controls that do not harm beneficial species. For example, the elimination or reduction of the use of broad-spectrum, persistent pesticides can allow soil-living predators (e.g. beetles – see page 59) to survive and reproduce.

When resident natural enemies are insufficient, their populations can sometimes be increased (augmented) through the purchase and release of commercially available beneficial species. There are commercially available suspensions or formulations using living microorganisms, such as bacteria, fungi, viruses or nematodes (see Chapter II) for the biocontrol of slugs, ants, flies (e.g. fruit flies), caterpillars, etc. The type of organism used is dependent on the pest population to be controlled. For example, the entomopathogenic nematode *Steinernema scapterisci* (see pages 46-47) can be applied to control some mole crickets (*Scapteriscus* spp.).

Mole crickets are pest insects living in the soil. However, it is possible to use another soil organism, the nematode *Steinernema scapterisci*, to reduce their populations. (MYO)

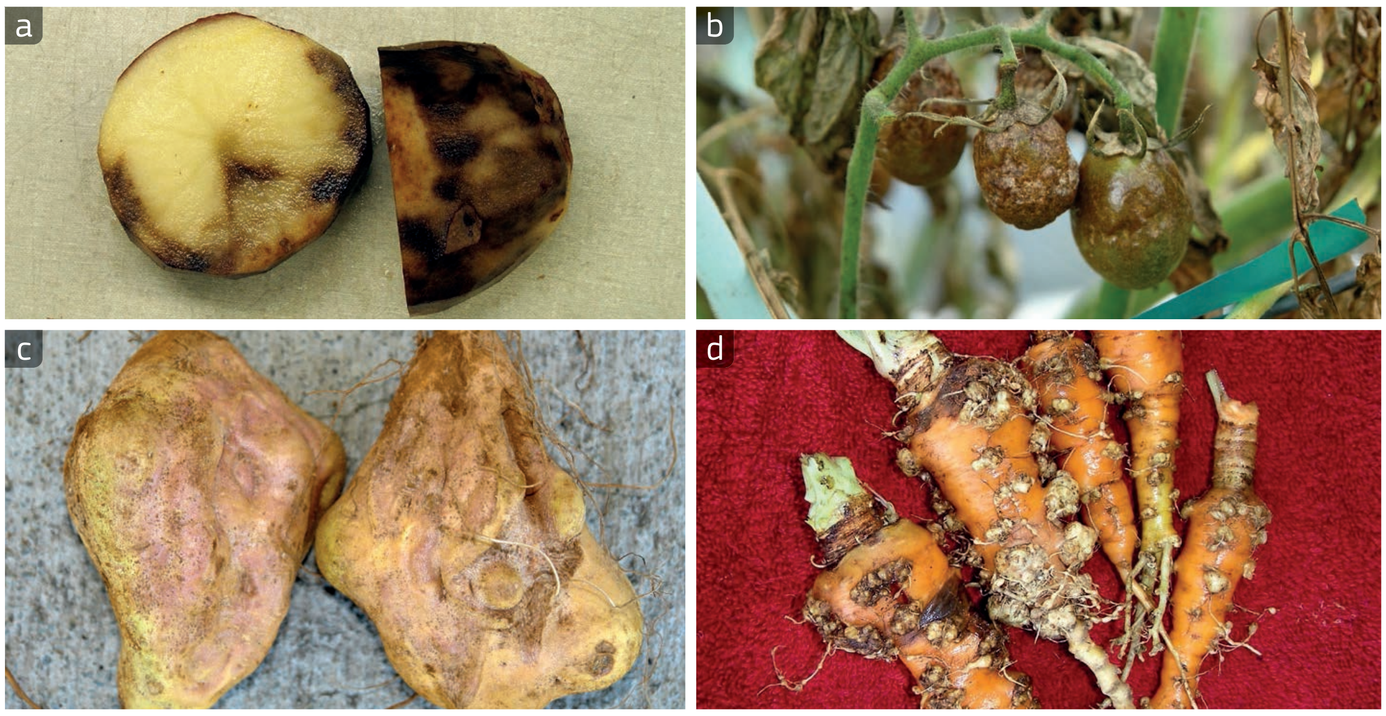
Classical biological control, also called importation, is primarily used against exotic pests that have inadvertently been introduced from elsewhere. Many organisms that are not pests in their native habitat become unusually abundant after colonising new locations without their natural controls. Researchers go to the pest's native habitat, study and collect the natural enemies that kill the pest there, then transport promising natural enemies back for testing and possible release. This type of practice needs particular attention as the introduction of new species might have negative impacts on the ecosystem.

Plant pathogens and pests

- A pest is an organism that has characteristics regarded as injurious or unwanted. Plant pests are herbivores (e.g. insects) that extensively eat plants, thus damaging them.
- A pathogen is a biological agent that causes disease or illness to its host. Plant pathogens are the microorganisms (e.g. bacteria and fungi) that cause plant diseases.

Suppressive soils

Although extensively studied, pathogenic interactions represent only a fraction of the overall plant-microbe interactions. The majority of plant-microbe interactions are either commensalistic or mutualistic (see box on page 33). The vast majority of plants usually benefit from these microbial associations in terms of growth enhancement, nutrient uptake, disease reduction and/or stress reduction.



Some of the effects of plant pathogens that live in soil. (**a–b**) *Phyophthora infestans* responsible for the late blight on potatoes and tomatoes. (**c–d**) Sweet potatoes and carrots affected by nematodes of the genus *Meloidogyne* show deformations and outgrowths called root-knots. (BMI, SCN, AKK)

Besides these examples of biocontrol strategies realised through human interventions, there are also cases of natural biocontrol, such as predatory and herbivorous mites (see page 49). Phytophagous (plant-eating) mites are a serious threat to their host plants; in the absence of predators they tend to overexploit their food source. To prevent such a crash and maintain as much leaf area as possible ,host plants may defend themselves in various ways, one of which is to increase the effectiveness of a group of natural enemies, the predatory mites, of the phytophagous mites. Predatory mites locate herbivorous mites, their prey, using herbivore-induced plant substances that the plant releases when the herbivorous mite starts feeding on it. In so doing, plants can activate their own bodyguards as soon as any damage is inflicted.

With regard to plant pathogens, it has been shown that the beneficial microbes in soils, also known as plant growth-promoting bacteria (PGPB), can affect plant growth through different direct and indirect mechanisms (see pages 98-99). In particular, some examples of the indirect mechanisms, which can probably be active simultaneously or sequentially at different stages of plant growth, are related to the repression of soil-borne pathogens (through the production of hydrogen cyanide, siderophores, antibiotics and/or competition for nutrients). Although significant control of plant pathogens or direct enhancement of plant development has been demonstrated by PGPB in the laboratory and in the greenhouse, results in the field have been less consistent. Because of these and other challenges in screening, formulation and application, PGPB have yet to live up to their potential as commercial inoculants. Recent progress in our understanding of their diversity, colonisation ability, mechanisms of action, formulation and application should facilitate their future development as reliable components for a more sustainable regulation of plant diseases.

It has also been suggested that plants can specifically attract microbes for their own benefit. This selection process allows for the recruitment of different groups of plant-associated microbes possessing general plant growth-promoting traits. Once recruited, these microbes undergo host-specific adaptations, the outcome of which is a highly specialised mutualism. Such mutualisms may make plants better able to tolerate plant-associated microbes without recognising them as pathogens; while the microbes, in turn, become more responsive to the plant's metabolism.

Suppressive soils have low levels of plant disease even though a pathogen is present. Soil biodiversity may be a primary factor in disease suppression. (AMI)

The plant transformer

- *Rhizobium radiobacter* (previously known as *Agrobacterium tumefaciens*) is a soil bacteria known as the causal agent of crown gall disease (also known as plant tumour) in over 140 species of plants. It is a member of the family Rhizobiaceae, which also includes the nitrogen-fixing legume symbionts that are beneficial bacteria for plants.
- The infection process of this bacterium consists of the transfer of a portion of its DNA (see box on page 30) into plant cells. This DNA contains genes that can generate the production of nutrients for the bacterium. The inserted DNA also contains genes that lead to the production of plant hormones responsible for the formation of the plant tumour.
- The DNA transmission abilities of *Rhizobium* have been vastly explored in biotechnology and molecular biology as a means of inserting foreign genes into plants (genetic transformation). This possibility was first described in 1977 by researchers from Ghent University in Belgium.

Rhizobium radiobacter is a soil bacterium that infects plants and leads to the formation of galls. These outgrowths are caused by an abnormal division of plant cells and also known as plant tumours. (DMU)

The diversity of microorganisms in soil is critical for the maintenance of soil health and quality, as a wide range of specific soil microorganisms play important roles in the suppression of soil-borne plant diseases and in plant growth promotion in agriculture. In fact, all natural soil possesses some ability to suppress the activity of plant pathogens thanks to soil microorganisms (general disease suppression). 'Specific suppression' occurs when specific microorganisms lead soils to be suppressive against a disease. Development of disease suppressiveness in soils has been reported for many diseases, including potato scab caused by *Streptomyces* spp., *Fusarium* wilt disease of several plant species, *Rhizoctonia* damping-off disease of sugar beet, and the take-all disease of wheat caused by *Gaeumannomyces graminis* var. *tritici*.

Supporting services – Soil formation and maintenance

Soil formation

As soils form, mature and age, they pass through a number of different stages, each of which is associated with specific species composition and structure in soil communities and plants. Soil biodiversity actively contributes to the transition from one stage to another, thus contributing to the formation of soils as one of the main factors that supports habitats (see box to the right) for itself and other living creatures. [66, 118]

Stage 1

In Stage 1, bedrock is exposed and weathering begins. Living communities are essentially comprised of microorganisms that form bacterial and algal crusts (biocrust – see page 73) and other structures, with a progressive development of a food web mainly comprised of invertebrate microfauna: protists, nematodes, rotifers (see pages 36-37, 45-47), plus a few mesofaunal components: collembolans and mites (see pages 49-50). Stage 1 is observed, for example, in the years following volcanic deposition or the recent exposure of rocks after glacial retreat due to melting. Depending on climatic conditions, this stage may only last from a few years to decades (e.g. tropical lava deposits) or persist for undefined periods of time (e.g. polar ecosystems).

Plants then appear, at first in the form of mosses and ferns, plus a number of pioneer plants (such as species of the family Bromeliaceae, e.g. pineapple, in the humid tropics or Ericaceae, e.g. heather, in temperate areas). Accumulation of organic matter from their dead materials allows for the development of a first horizon (the A Horizon – see page 10), which is a mixture of fine-textured mineral elements and organic matter. While organic matter produced in these ecosystems is often of a rather low quality, it tends to accumulate on the soil surface, forming increasingly thick accumulations in which a wide diversity of arthropoda, such as hexapods (see page 31), myriapods (see page 57) and other invertebrates of the litter transformer group (see page 112) build remarkably large and diverse communities.

Lixiviation vs. eluviation vs. illuviation

- Lixiviation and eluviation are both processes that influence soil formation.
- Lixiviation, also known as leaching, is the loss of mineral and organic solutes as a result of percolation, which is the movement and filtering of water through soil pores.
- Eluviation is the loss of mineral and organic colloids as a result of percolation. Eluviation differs from leaching in that it affects suspended, not dissolved, material.
- Illuviation, however, is the accumulation of dissolved or suspended soil materials in one area or layer as a result of lixiviation or eluviation from another.

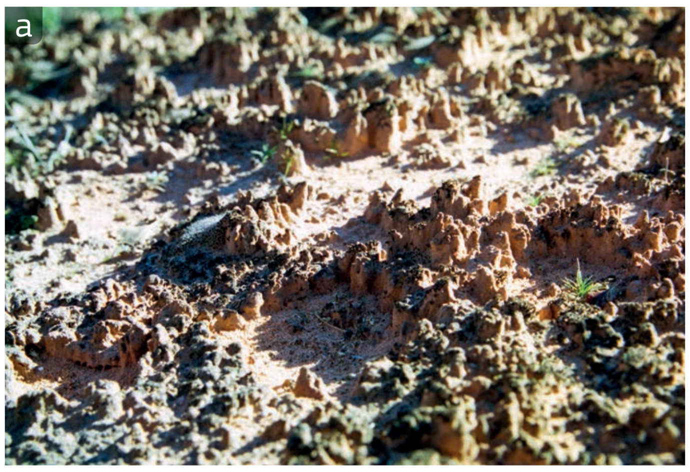
Stage 2

In Stage 2, deeper soils allow for the development of bushes and trees. The weathering of the bedrock is accelerated by the direct effects of roots, or indirectly by the effects of different substances (e.g. organic acids) issuing from the decomposing leaf litter. Lixiviation (see box to bottom left) of organic acids from decomposing litter triggers the migration of clay minerals to the bottom of the profile where they form a B horizon, causing an eluviated E horizon to appear.

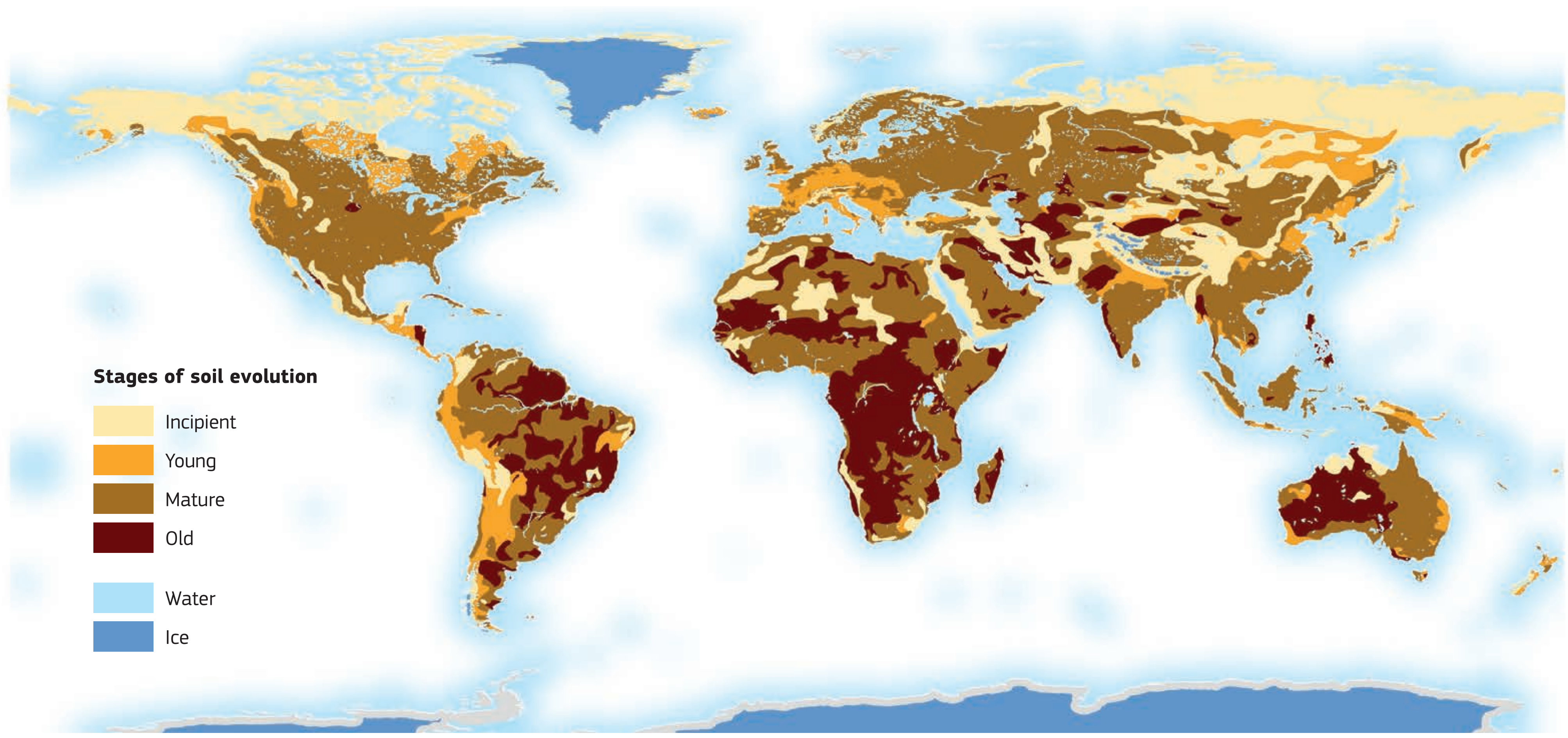
Vegetation is often dominated by coniferous trees and litter accumulates that form a very active litter system in which fungi (see pages 38-41), collembolans, mites and enchytraeids (see page 48) are abundant. These soil organisms are litter transformers and play a vital role in the decomposition and humification (production of humus – see page 106) of all types of plant and animal remains. Soil in the A horizon is often acidic, which may limit the activity of ecosystem engineers, especially earthworms (see page 58).

What is a habitat?

- A habitat is a geographical unit that effectively supports the survival and reproduction of a given species or of individuals of a given species.
- The biological composition and the abiotic factors therein describe the geographical unit.
- Other organisms include the plants, animals, fungi, bacteria, viruses and protists that also live in a given habitat.
- Abiotic factors include the soil's physical and chemical properties, water availability, temperature, sunlight, air quality and landforms that facilitate resting, foraging, nesting, mating and other activities.
- The term habitat is one of the most misused and poorly defined in the field of ecology. This is due to the fact that some authors have emphasised the geographical nature of the term, while others have stressed the organism associations inherent in the definition.
- Actually, geographically associated species and abiotic factors are all inextricably linked to the concept of a habitat.



In Stage 1 of soil formation, (**a**) biocrust contains the first living communities (e.g. bacteria and lichens). Then food webs of micro-faunal organisms, such as (**b**) rotifers, appear. In stage 2, soils are often covered by (**c**) coniferous plants that create a litter system that allows more complex communities of mesofauna, including (**d**) collembolans, to proliferate. (AQ, WVE, NAT, AM)



World distribution of stages of soil evolution from 1 (incipient) to 2 (young), 3 (mature) and 4 (old impoverished). (RCR, ISM, JRC)

Stage 3

Stage 3 marks the full maturity of the soil system as vegetation reaches full development and soil communities reach their maximum levels of activity and diversity. Plant communities have become fully established, and deciduous trees produce increasingly high-quality organic materials that stimulate biological activity in the soil. [66, 118]

Ecosystem engineers become predominant and accumulate their biogenic structures (mainly earthworm, ant and termite galleries, casts and constructions) in their respective functional domains of influence. These are especially earthworms of the anecic and endogeic groups (see page 58) that exhibit deep burrowing activity and mix the soil (known as 'bioturbation'). The same activity is also carried out by other organisms, such as ants, termites and beetles (see pages 54-55, 59). The dominant group of organisms performing this function varies among ecosystems. Root systems penetrate into deeper soil horizons using channels created by these invertebrates. This improves the resilience (adaptability – see page 97) of tree communities. Natural soil fertility is at its maximum, as is the provision of other soil system services, such as:

a. hydrological functions, including enhanced infiltration and water retention in deep soils, facilitated by numerous connected biopores (see page 107)
b. climate regulation promoted by carbon accumulation in woody biomass and soil organic matter, since biomass production and sequestration of organic matter in stable bio-aggregates are at their maximum (see pages 102-106)
c. plant growth support (see pages 98-99) and biological control (see pages 108-109) are maximised due to the dense populations of generalist predators and diversity in pest communities which limits the impact of the most aggressive ones; increased robustness of plants due to optimal development of mutualist organisms, such as mycorrhizal fungi (see page 40) and symbiotic bacteria in their rhizosphere

Stage 4

In Stage 4, soil becomes impoverished due to accelerated migration of critical elements of fertility, such as organic matter and iron oxides, to deeper soil horizons. Plant communities change and shift back toward less exigent forms, such as coniferous forests or heathland shrubs. Earthworms and most other ecosystem engineers are progressively eliminated by increasing acidity and low quality of the remaining organic matter.

Later on, highly weathered soils no longer sustain high levels of biomass production, and soil communities progressively lose elements, returning to patterns comparable to those observed at initial stages, although with much deeper soils. Ecosystem services are provided at lower rates, although with large differences among the different ecosystem service categories. While support to plant production significantly decreases, hydrological function may still be at its highest due to soil depth. Biological control may still be supported at relatively high levels due to the high biodiversity of specialist organisms selected through stressful conditions.

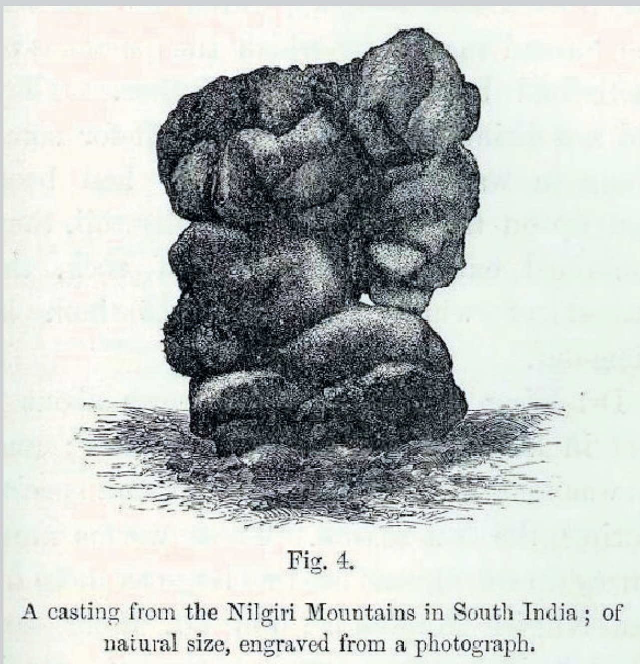
In Stage 3 of soil formation, (**a**) soils are mature and have a well-established soil community, which also includes ecosystem engineers, such as (**b**) ants. In stage 4, (**c**) soils become impoverished, as does the soil-living community, which reverts to being relatively simple and mainly composed of microorganisms, such as (**d**) bacteria (the photograph shows a colony of bacteria surrounded by soil particles). (NTA, CHY, MTN, FW)

Distribution of soil development stages across the Earth

The evolution of soils is a very slow process. Under temperate conditions it can take about 20 000 years to create one metre of soil. When the climate is less favourable, evolution is even slower and can even stop at early stages when drought or excessively cold temperatures limit the progress of biological activity and other processes. Soil formation, scientifically known as 'pedogenesis', may also change its course when natural or human-induced events modify any of the three major drivers (i.e. soil biodiversity, bedrock or climate) involved in the process. As a result of different soil communities, geological histories and climatic conditions, soils of the world show a wide diversity in their stages of development (see map page 110).

Charles Darwin and earthworms

- Charles Darwin (1809-1882) was an English naturalist and geologist, best known for developing the theory of evolution.
- His last scientific book was entitled 'The Formation of Vegetable Mould through the Action of Worms, with Observations on their Habits'.
- This book represents the first significant work on soil formation through the casting activity of earthworms.
- In the conclusion, Darwin writes that worms 'have played a more important part in the history of the world than most persons would at first suppose'.



One of the original illustrations, drawn by Charles Darwin, showing an earthworm casting from the Nilgiri Mountain in South India. (GER)

Earthworms from space

- The South African giant earthworm (*Microchaetus rappi*) is one of the largest earthworms, with an average length of about 1.5 m.
- They have created a unique habitat in the Eastern Cape Province of South Africa known locally as 'kommetjies', a wavy or undulating pattern of hollows and mounds. After heavy rains, the hollows can fill up with water.
- The exact mechanism for the creation of this landscape, which is visible on satellite imagery, are still being debated. One theory is that the mounds are located in shallow soils where the presence of an impermeable layer (either bedrock or plinthite – see page 22) restricts the movements of the worms. Such soils tend to be very wet after summer rainfall before entering a relatively long period of drought.
- When active, the feeding end of the worm would be located in the more humid part of the soil, with its casting end in more aerated conditions. Large worms would be able to collect more soil material from the wet parts and deposit it on the drier parts. Over time, this aspect would result in a self-sustaining landscape where the scale of the mounds reflects the size of the worms.

Disturbed ground due to the burrowing activities of the South African giant earthworm (*Microchaetus rappi*) is visible on satellite imagery. Buildings and roads give a sense of scale. (GOG)

Supporting services – Soil formation and maintenance

The age of soil

As soils evolve, they get deeper and distinct horizons develop. The first horizon (**INCIPIENT**) forms where organic matter is mixed with minerals detached from the weathering bedrock. Thereafter, another distinct horizon forms (**YOUNG**) where clay, base and, ultimately, organic matter accumulate (**MATURE**). Finally a leached horizon (**OLD**) forms. During this process, soil becomes progressively impoverished in nutrients.

Soil communities comprise four major groups that have different relative importance and functions as soils mature.

Microorganisms are always present, although their composition may vary greatly, with large proportions of nitrogen-fixing algae and cyanobacteria in the earliest stages. Fungi are abundant when leaf litter is continuous and thick, whereas bacteria are more common in humid grasslands and cropped fields where earthworms are numerous.

Micropredators are comprised of a large diversity of small invertebrates of the micro- (< 0.2 mm) and meso- (0.2 to 2 mm) fauna that feed on microbial communities, thus regulating their composition and overall activity. They are the first group to develop in incipient soils, and may also be the only one left in severely degraded soils.

Litter transformers are invertebrates from the meso- and macro- (> 2 mm) fauna that live in and feed on leaf litter. They comprise a large number of micro- and macroarthropods that fragment and digest the partly decomposing litter left by the microorganisms. They are present whenever soil is covered with dead vegetation. They are most numerous and diverse in deciduous forests in temperate regions and in tropical forests.

Ecosystem engineers mainly comprise macroinvertebrates (ants, termites and earthworms), but also some mesofaunal groups (such as enchytraeids), able to cause intense bioturbation through active burrowing. By tunneling, they alter the soil space and create pores, channels and solid aggregate structures that constitute the habitat of other small organisms: microbial communities, and micro- and mesofauna. In the volume of soil that they control, also called their functional domain, they determine the composition and activity of microorganisms and the micro-predator food web.

While ants may be present in every type of ecosystem, with harsh climatic conditions and/or severe degradation, termites and earthworms are more dependent on stable conditions. Enchytraeids dominate wet and cold systems, such as moorlands. Ecosystem engineers are mainly present in well-developed soils at young and mature stages and tend to disappear in soils subjected to intensive agriculture.

The four main stages of soil evolution. Soil organisms play important roles in each stage. (PL, JRC)

Soil maintenance

Other ecosystem services provided by soils and their biota increase and are maintained as the ecosystem functions that they sustain gain in intensity. As described previously, it is possible to identify four stages in the evolution of soils, corresponding to the vertical arrangement of layers in a soil profile (see page 112). Because of their immaturity, developing soils do not provide significant contributions to soil system services. However, young soils are important for supporting plant growth since roots mainly develop in this layer. Mature soils may allow large amounts of water to infiltrate and to be retained in their pore spaces at different matric potentials, thus optimising supply to plants and, ultimately, allowing water to feed springs and rivers. Older soils play a key role in the control of the hydrological cycle thanks to their greater depth, where water tends to accumulate. [136]

Forces due to folding and faulting of the Earth's crust (orogenic processes) and erosion continuously bring new bedrock elements to the surface, and new soils are formed while old, highly impoverished soils are slowly disaggregated by erosion, reincorporated into the deep soil cortex by continental plate movements or buried below fresh volcanic deposits. As soon as they emerge above sea level, sediments and rocks start to be weathered by physical and chemical processes, and colonised by increasingly diverse organisms. Coexisting organisms progressively increase in their interactions as new species appear and biodiversity increases.

Coevolution for several hundred million years has led to the emergence of mutualistic interactions (see box on page 33) betewen micro- (e.g. fungi) and macroorganisms (e.g. plants) that enabled them adapt to two major constraints in soils: the difficulty to move and to find food in a very compact environment and the relatively low quality of the organic materials that comprise the majority of the available food sources. These relationships are crucial to maintaining the proper functioning of soils.

A mature soil profile can be maintained in this state for hundreds of years thanks to the action of soil-living organisms and stable climatic conditions. (NIL)

In conclusion, soil-living organisms have two major effects on and functions in soil formation and maintenance:

a. as active agents in soil formation, maintenance, organisation and dynamics through intense mechanical effects (bioturbation, burrowing, chemical transformation, transport and mixing of organic and inorganic elements)
b. as a source of organic matter (see page 106) through excreta, as prey and when dead. Organic matter has three major functions: 1) as an energy source for living organisms; 2) as a reactive building material of soil structure acting as a frame or glue in the formation of stable aggregates; 3) as a sizeable stock of carbon subtracted from the atmosphere (thereby also participating in climate regulation)

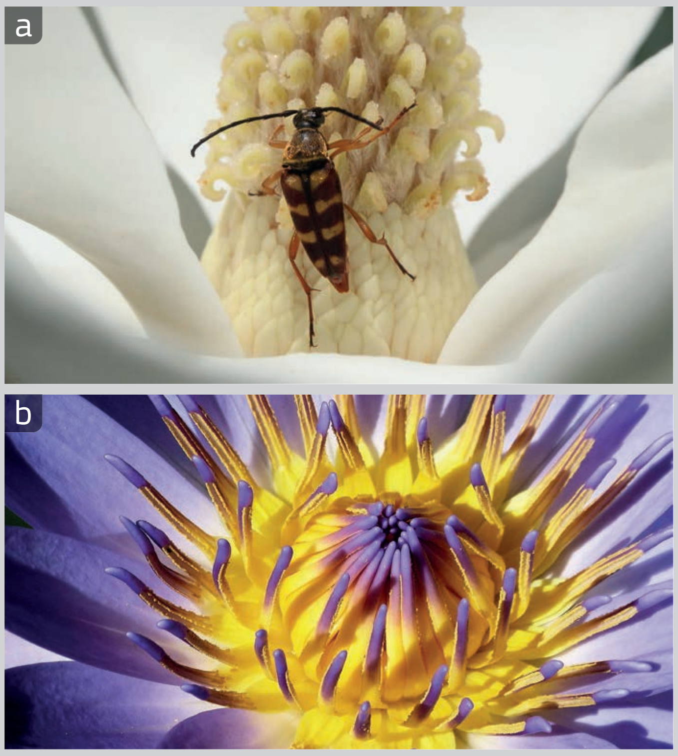
These two effects allow soils to be maintained in terms of both structure and fertility, thus resulting in the provision of other ecosystem services.

Soil biodiversity contributes to the continuous production of soil organic matter, which gives the dark colour to soil and is an important factor in soil fertility. (NRCS)

Different types of architectural formations, which contribute to the maintenance of soil structure, produced by soil-living organisms: (**a**) earthworms, (**b**) ants and (**c–d**) burrowing bees. (TRA, JIL, GNO, ITA)

Soil and pollination

- Beetles not only play a role in the formation and maintenance of soil through their shredding and burrowing activities. They also contribute to another ecosystem service: pollination.
- Most beetles that visit flowers are not there to sip nectar. Beetles often chew and consume parts of the plant they pollinate, and leave their droppings behind. For this reason, beetles are referred to as 'mess-and-soil pollinators'.
- Beetles were among the earliest prehistoric pollinators, and they continue to provide pollination services to flowers today. Fossil evidence suggests beetles first pollinated cycads. They began visiting flowering plants about 150 million years ago, a good 50 million years earlier than bees.
- Living beetles seem to prefer pollinating close descendants of those ancient flowers – primarily magnolias and water lilies. Although not many plants are primarily pollinated by beetles, those that do are called cantharophilous plants. Cantharophilous plants are often fragrant, giving off spicy or fermented scents that attract their beetle pollinators.
- The flowers that are visited by beetles are typically:
  - bowl-shaped;
  - white to dull white or green;
  - strongly fruity;
  - open during the day;
  - moderate nectar producers;
  - may be large solitary flowers (i.e. magnolias, pond lilies);
  - may be clusters of small flowers (e.g. goldenrods, *Spirea* spp.).



(**a**) Beetles are known as mess-and-soil pollinators because of their behaviour: they blunder around the flowers, such as (**b**) those of water lilies, chewing on petals, eating pollen and defecating. (DHI, SSA)

Cultural services – Natural capital

Value of soil biota

Natural capital can be defined as the world's stocks of natural assets, including geology, soil, air, water and all living things. It is from this natural capital that humans derive a wide range of ecosystem services that make human life possible. Ecosystem services provided by soil organisms have been presented in previous sections. With financial capital, when we spend too much we run up debt, which, if left unchecked, can eventually result in bankruptcy. With natural capital, when we draw down too much stock from our natural environment we also run up debts which need to be paid back. Poorly managed natural capital, therefore, becomes not only an ecological liability, but also a social and economic liability. Ultimately, nature is priceless. However, it is not valueless and there are many studies around the world that have tried to estimate our natural capital in financial terms. Since it is extremely difficult to assign a precise economic value, different kinds of values can be assigned to soil biodiversity. [138]

Many of the ecosystem services identified by the Millennium Ecosystem Assessment are driven by the soil biota, often resulting from the interactions between organisms or groups of organisms within the soil. Efforts have been made to place a monetary value on such services to give an indication of the cost that we would face should we have to perform these services ourselves. However, such efforts tend to overlook the fact that the vast majority of the services do not occur in isolation, but rather are intertwined, with some organism groups performing several different services, and many of the services culminating as the output of the interaction between several different groups of organisms. This means that in many instances it would not be technologically possible for us to perform the services ourselves. Furthermore, it can be argued that any study that tries to place a total value on all soil-based ecosystem services is inherently flawed because of the complexity of the soil environment.

Soil-based ecosystem services are vital for our continued existence on Earth; without them we could not survive. Therefore, the value of such services are, for all intents and purposes, infinite. Here we focus on the value of soil biodiversity, which includes economic value but also covers a much wider scope. Soil biodiversity and its associated ecosystem services can be valued in different ways depending on the perspective from which they are considered, including the following:

- functional value. This relates to the natural services that the soil biota provide, the associated preservation of ecosystem structure and integrity and, ultimately, the functioning of the planetary system through connections with the atmosphere and hydrosphere. For example, less value may be placed on degraded soils due to their reduced functioning in terms of storing carbon, cleaning water, and preventing soil erosion and its associated environmental problems
- utilitarian value (i.e. 'direct use'). This covers the commercial and subsistence benefits of soil organisms to humankind. Examples include the provision of food by soil organisms, such as mushrooms, as well as biotechnology, such as the provision of antibiotics
- intrinsic value (i.e. 'non-use'). This comprises social, spiritual, aesthetic, cultural, therapeutic and ethical benefits. For example, most people agree that there is a value in having green spaces within cities even if we do not live in those cities or use the green spaces. The same is true of natural parks, even though we may not visit and use such natural parks ourselves. Furthermore, hospitals and nursing homes with green spaces have been shown to facilitate the recovery of patients. Such spaces have an 'intrinsic value', and as they are reliant on the functioning of belowground communities (i.e. the soil biota), they too must have an intrinsic value
- bequest value (i.e. 'option' or 'serependic'). This relates to planetary functions for future generations. It concerns the unknown. The idea is that there is value in not depleting soil biodiversity so that future generations can benefit from the services it provides. This is true in terms of the ongoing survival of humans on Earth. In addition, many novel compounds, such as antibiotics, have been isolated from soil organisms (e.g. bacteria). The vast majority of soil bacteria remain to be fully described, and so it seems likely that there are still many useful novel compounds yet to be discovered. Therefore, there is value in maintaining soil biodiversity so that such compounds still exist for discovery by future generations

Economic value: the most expensive soil organism

- The most expensive food in the world is a soil fungus.
- The white truffle (*Tuber magnatum* Pico) is a fungus that establishes an ectomycorrhizal symbiosis with trees (see page 40).
- White truffles have a limited distribution in southern and central Europe, occurring in Italy, Switzerland, Croatia, Slovenia and Serbia.
- The life cycle of this fungus is complex. Despite many efforts, attempts to 'domesticate' the white truffle have not yet been successful.
- The most refined white truffle is from the Piedmont region (Alba) in the northern Italy. It is known as the white truffle.
- White truffle prices can reach into the hundreds (or even thousands) of Euros per kilogram, depending on the harvest.
- Each year the price of the white truffle is established at the annual Worldwide Alba Truffle Auction.
- In 2007, a white truffle believed to weigh around 750 grammes was sold for US$208 000 (i.e. 2 173 dollars per gramme – approx. €2 000).

The white truffle, a soil fungus, is one of the most expensive foods in the world. (EKI)

The value of soil biodiversity can be considered from different points of view. (**a–b**) Provision of clean drinking water is an example of a functional value attributable to soil biota. (**c–d**) The utilitarian value is represented by food. (**e–f**) The bequest value is related to the need to preserve soil biodiversity for future generations. (**g**) The beauty of a landscape, also thanks to the action of soil organisms, shows the intrinsic value of soil biota. (RKA, DFAT, CGU, DEN, NP/CIAT, MMP, BAR)

Food security

It is widely accepted that the near future will see the development of new microbial strains and soil-dwelling organisms that offer potential solutions to problems relating to food shortage. Already, the application of biotechnology in agriculture has resulted in new crop varieties with increased resistance to pests and diseases (see pages 100-101), as well as with higher nutritional values (e.g. Golden Rice) (see box below). Nevertheless, such progress does not come without drawbacks, some of which remain controversial. Strict regulations and protocols have already been implemented to minimise potential hazards associated with genetic manipulation and the spread of transgenic organisms, among which the direct threat to human and animal health and the risk to 'natural' biodiversity are perhaps of most concern. There is, therefore, strong pressure and incentive to utilise natural biodiversity to meet the ever-growing consumer demands for such products in our increasingly environmentally focused society. [137]

In the current challenge of feeding a continuously growing population (see page 18), soil biota may also represent an important ally from another perspective. Since 2003, the United Nations Food and Agriculture Organization (FAO) has been working on topics related to edible insects in many countries worldwide. For example, 32 Amazonian ethnic groups consume more than 100 soil invertebrate species. Edible insects contain high quality proteins, vitamins and amino acids. Insects have a high feed conversion ratio (FCR); for example, crickets need six times less feed than cattle, four times less than sheep, and half of what pigs and chickens require to produce the same amount of proteins. In addition, they emit less greenhouse gases than conventional livestock. Therefore, insects are a potential source of proteins, either for direct human consumption, or indirectly in processed foods (using proteins extracted from insects); and as a protein source in feedstock mixtures. As many soil insect larvae (see page 60) are already consumed, soil biota may represent a source of food that would be worth further investigation.

Golden Rice

- A type of genetically modified organism proposed for use in agriculture is the augmentation of the nutritional value of a given crop.
- An example of this was the production of 'Golden Rice' in 2000.
- This rice contains the beta-carotene gene (a precursor of vitamin A) inserted into its edible parts, hence the golden colour.
- The production of beta-carotene is possible thanks to a genetic modification that consists of the introduction of two genes. One gene is from the daffodil (*Narcissus pseudonarcissus*), and the other from a soil bacterium.
- The genetic modification is carried out with the goal of countering the deficiency of dietary vitamin A that occurs in large parts of the world.
- The most common symptom of vitamin A deficiency is night blindness, in which case it is difficult for eyes to adjust to dim light.
- Each year vitamin A deficiency is estimated to be responsible for the death of more than 650 000 children under the age of five.
- In 2009, research on a group of adult volunteers concluded that 'beta carotene derived from Golden Rice is effectively converted to vitamin A in humans'.

Golden rice contains beta-carotene. This molecule gives the characteristic golden colour to the rice grains. (IRRI)

Soil biodiversity and crime scenes

- Using soil is not new to police investigations. Forensic soil science has been used for more than 150 years. Soils can be examined using a number of different physical and chemical analyses (e.g. colour, particle size and mineral content). However, the geographic precision of these techniques is often limited. [139]
- Each patch of soil has its own unique DNA signature (see box on page 30) based on the fungi, bacteria and other organisms living in it. This is valuable information for scientists working in forensics.
- A simple experiment was carried out to assess the applicability of soil DNA in forensic investigations. A shovel was used to dig a shallow grave before being placed into a car boot alongside shoes worn at the time. Six weeks later, the DNA of the fungus, plants, and organisms living in the soil stuck to the shoes and shovel was recovered, and compared to DNA detected in soils from multiple other locations. The unique signature of the soil organisms placed the soil samples recovered from the shoes and shovel just metres from the crime scene.
- This study is one of the first to demonstrate that soil DNA sequencing could precisely distinguish between physical locations where current methods offer limited resolution.

Recent studies demonstrate that DNA of soil-living organisms can be used in real-life applications to track criminals weeks after the crime and accurately place them at crime scenes. (AMD)

Human heritage

Much of the evidence of human heritage remains buried within the soil, awaiting discovery and study by archaeologists and palaeoecologists (scientists that study past environments and ecosystems). The degree of preservation depends very much on the local soil characteristics and conditions. Soils with extreme characteristics (e.g. very acidic, very alkaline or waterlogged with low levels of oxygen) provide an ideal environment for preserving organic remains. Soil organisms play a key role in soil formation processes (see pages 110-113); therefore, they can indirectly influence the preservation of archaeological evidence. However, soil biota can also have negative effects, as intense soil microbial activity can lead to degradation of any type of material, including objects of historical interest. Nevertheless, the terrestrial subsurface is generally characterised by low concentrations of organic carbon and oxygen and, by comparison with surface soils, relatively few microorganisms (see page 73). Another important aspect to consider is the material to be investigated. Some biological materials (e.g. pollen, leather and wool artefacts) are easily degraded by soil organisms; whereas, under other circumstances, it is possible to take advantage of the decomposing action of soil biota. For example, recalcitrant residues from wood decomposition are important marks of the past presence of the so called 'post holes', which are spaces once filled by poles to sustain buildings or other structures. Archaeologists can use their presence to plot the layout of former structures as the holes may define their corners and sides. Despite everything previously described, there are very few measurements of soil microbial parameters at ancient archaeological sites, and the general applicability of these observations to other archaeological sites remains unknown.

Any soil disturbance, such as by drainage or ploughing, may change the optimal conditions for archaeological conservation and, therefore, lead to the rapid decay and loss of material. Archaeologists use these historical artefacts and the layers in which they are preserved to reconstruct the communities that produced them and the environments in which they lived. But to do this, the soil layers must remain undisturbed.

An archaeological dig at a site of a third century battle between Germanic and Roman troops in Harzhorn in northern Germany. In many cases, material discovered in the soil is the only evidence of historical events or of how people lived. (AHI)

Educational value

Many studies have shown the importance of playing with soil and the positive effects of soil-living organisms (e.g. our beloved earthworms) on children's health. Some of the reasons are:

a. a bacterium naturally found in soil, *Mycobacterium vaccae*, activates the neurons that produce serotonin – a key chemical in many bodily functions, as well as a natural anti-depressant
b. the typical behaviour of children is to always put dirty things in their mouths. There may be an evolutionary reason for such a universal behaviour, a finding that science seems to corroborate. Called the 'hygiene hypothesis', many researchers have concluded that the millions of bacteria, viruses and other organisms that enter the body with every spoonful of soil 'eaten' are necessary for the development of a healthy immune system
c. the term 'nature-deficit disorder' describes a common condition of younger generations, due to the lack of physical experiences in the natural world, which have been replaced by more solitary and unstructured activities, like playing video games. Children are not given enough opportunities to play outside, which has now been linked to attention disorders, depression and obesity. By contrast, children who play outside laugh more, which means they are happy. It also means their blood pressure and stress levels are lower. They grow in their character development by becoming more adventurous, more self-motivated and more able to understand and assess risks

Scientific studies have demonstrated that playing with soil, as well as the effects of soil-living organisms, are good for human health. (TS)

Conclusions

Soils that sustain high levels of biodiversity are increasingly endangered, mostly due to anthropogenic intervention (see Chapter V) despite their demonstrably high value, as shown above. Protection, as well as sustainable management and exploitation of soil biodiversity, must be addressed from a conservation perspective (see Chapter VI). Measures to assess threats to soil biota and, consequently, to preserve soil biodiversity will undoubtedly contribute to sustaining environmental and human health and continue to enrich the human condition and way of living. Soil biodiversity is too valuable not to be protected!

CHAPTER V – THREATS






Soil biodiversity is potentially under threat because of several pressures acting on soil, ranging from intensive agriculture, pollution, desertification and land degradation, soil erosion and fire to deforestation. Despite all this, the consequences of the reduction or loss of soil organisms are still poorly studied and, therefore, will need further attention in the future. (LPL, RHO, MFR, OPF, MLE/NPS, MKE)

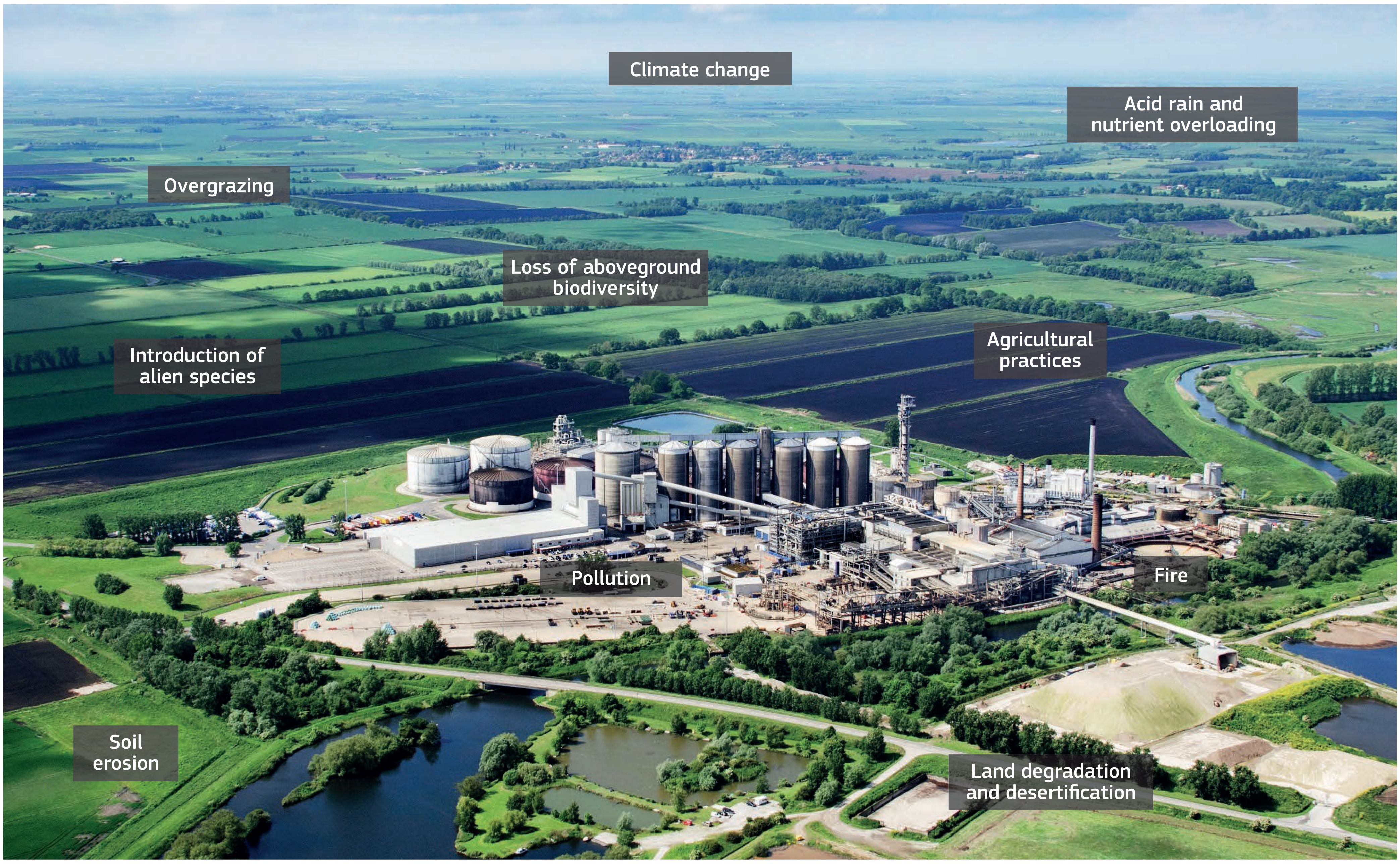
Introduction

The extraordinary ability of humans to modify the environment in order to meet their own needs underlies the success of humans as a species on Earth. Since the onset of agriculture, humans have altered the local diversity of plants by clearing land and cultivating selected plant species that were desired for food, feed, clothing and building material. The industrial and green revolutions, with the mechanisation of labour and the discovery of how to produce mineral fertilisers and chemicals to control weeds, pests and diseases, resulted in dramatic increases in crop yields. Unfortunately, these fundamentally different methods of land management have also generated unwanted side effects. [140]

In the 1960s, with the publication of Rachel Carson's Silent Spring, scientists, the general public and policymakers began to realise how pesticide use could cause unforeseen adverse effects throughout the food chain. The disappearance of plant species also has effects on belowground biodiversity and soil food webs. Furthermore, pollutants that end up in soil as a result of oil spills or mining activities can impact soil organisms and the myriad of ecosystem functions provided by soils. Similarly, the physical disturbance of soils, including sealing, compaction and erosion, has the potential to eliminate many belowground taxa.

Soils harbour tremendous biodiversity. However, proliferation and functioning are dependent on their chemical and physical soil properties. As for all life forms, water availability is of utmost importance for life in the soil. Over the past twelve decades, global climate change has altered precipitation and temperature regimes, which impact soil biodiversity both directly and indirectly through their impact on primary productivity and plant diversity. In many cases, the enormous biodiversity found in soils may serve as a source of organisms which can adapt to the new conditions and may even help to improve adverse conditions for plant growth. Awareness of soil biodiversity and its functional importance will enable the development of more sustainable management practices. By more carefully considering how soil biodiversity may be affected by management practices, and adapting accordingly, we will be able to better preserve belowground diversity and the important functions of these communities in order to enhance and maintain soil health.

(**a**) Loss of aboveground diversity, (**b**) soil compaction, (**c**) intensive agricultural practices and (**d**) pollution are some of the threats to soil biodiversity presented in this chapter. (AER/CIFOR, LCH/USDA, USB, CAD)



Many of the threats that can potentially alter soil-living communities are easily identifiable when looking at the environment around us. Most of the pressures are a result of human activities, such as farming, industrial activities and climate change. (JFI, JRC)

Loss of aboveground biodiversity

Plant-soil interactions

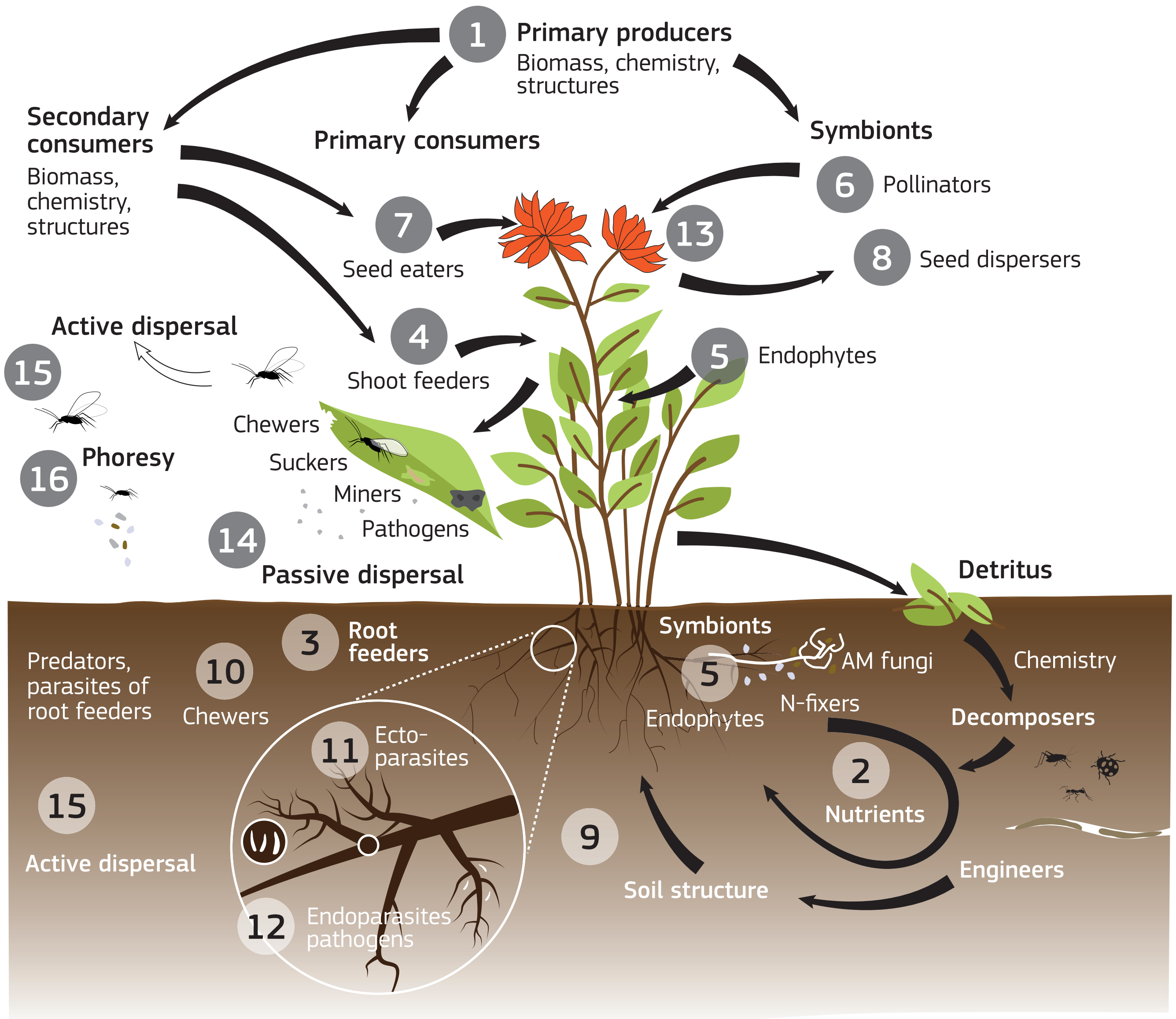
Aboveground biodiversity refers to all the organisms that live above the soil. The starting point of all terrestrial food webs (see page 96), both above- and belowground, are primary producers, mostly plants and algae. Through photosynthesis (see box on page 35), these organisms transform inorganic compounds of carbon dioxide (CO_2) from the atmosphere and water (H_2O), together with mineral nutrients from the soil, into organic compounds in the form of their own plant tissues. All heterotrophic organisms (see page 30) depend on these primary producers to obtain their energy and nutrients. The question remains, however, how above- and belowground biodiversity are related and whether loss of aboveground biodiversity also implies loss of belowground biodiversity. [141]

When looking at the plants in woods, grasslands or parks, it becomes clear that aboveground plant species are different in their shape, colour and smell (i.e. are physically and chemically different). Similarly, albeit less well known, plant species also differ belowground in the morphology and chemistry of their roots (see page 43). As a result, the composition of soil organisms also differs between plant species such that a higher diversity in soil biota is positively correlated to a higher diversity in plants. Conversely, there is a risk of losing species of belowground organisms with decreasing plant species richness. It is important to note that some plant species are much more diverse than others, meaning that losing certain plant species from an ecosystem can have much greater impacts on belowground biodiversity than you would expect from the change in plant species number. This, for example, happens when a plant species with unique associations with soil fungi (see pages 38-41) disappears.

Deforestation in numbers

- A recent study estimated that the total number of trees on our planet is approximately three billion (3×10^{12}). [142]
- This means that there are 422 trees for every person on Earth.
- This more accurate estimate of the number of trees on the planet was based on scientific data gathered from all continents except Antarctica.
- The study also reported that 15 thousand million trees are cut down each year.
- In the 12 000 years since farming began spreading across the globe, the number of trees on our planet has fallen by almost half.

Given the vast diversity of soil organisms and, in comparison, the lesser number of plant species, it has been argued that many of the species that live in the soil most likely behave as generalists rather than as specialists with regard to the food they consume. Biodiversity studies do provide some support for this idea given that with increased plant species richness the increase in species richness of soil organisms is especially notable at the lower end of the plant-species-richness gradient. The increase tends to level off at high plant diversity, depending on the group of soil organisms. For example, nematode diversity (see pages 46-47) may increase (or decrease with plant species loss) at a faster rate than the diversity of collembolans (see page 50).

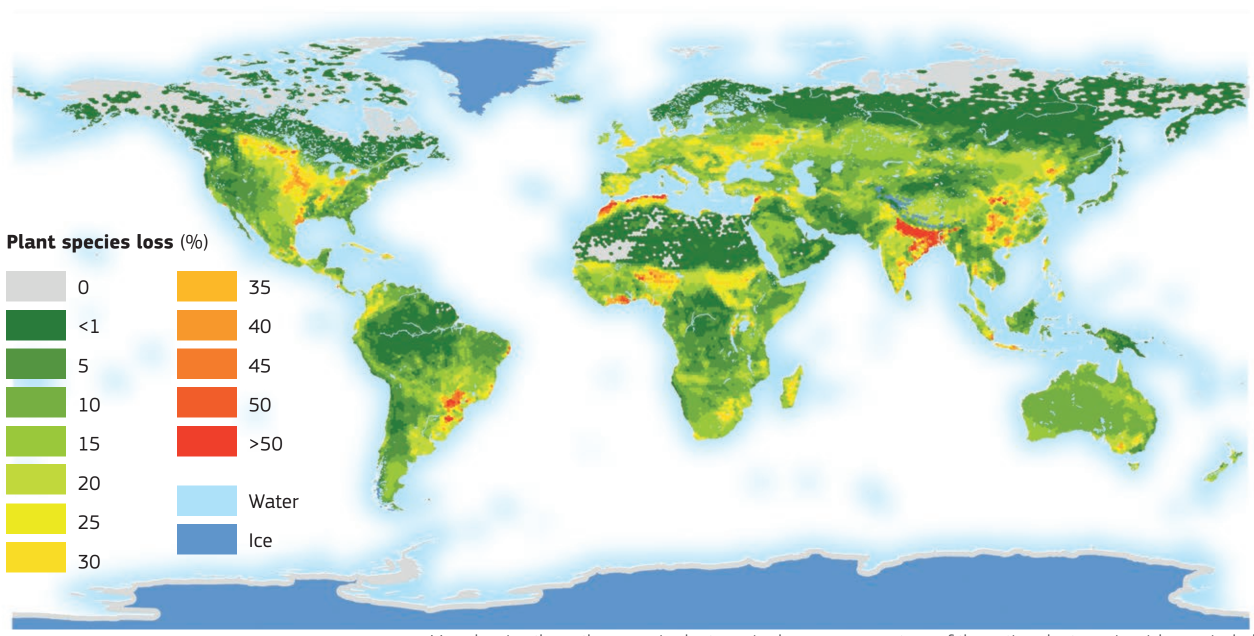


Plant communities (**1**) drive the abundance and diversity of other aboveground organisms, although these plant characteristics depend on the activity of soil functional groups, such as decomposers and symbionts, which make nutrients available (**2**), and on belowground and aboveground herbivores and pathogens (**3–4**), which reduce plant growth. Heterotrophic organisms that interact with plants affect plant metabolism by feeding on roots (**3**) or shoots (**4**) or living symbiotically in shoots, leaves or roots (**5**). In the longer term, pollinators (**6**) as well as seed eaters (**7**) and seed dispersers (**8**) affect the persistence of the plant species and, consequently, the specialist organisms associated with it. Soil organisms are constrained in their mobility and, as a result, organisms interacting with a single plant root system are subsets of the total species pool present in the surrounding soil (**9**). Although active roots have high turnover rates and are distributed throughout the soil, root herbivores and pathogens (**3**) can account for this 'unstable food' source by being relatively mobile generalist feeders (**10–11**), similar to many aboveground chewing insects and free-living suckers, by adapting a specialised endoparasitic plant association (**12**) or by having an aboveground life phase enabling targeted active dispersal (**15**). Aboveground plant structures might be easier to find than roots, and although the availability of more specific aboveground plant tissues [e.g. flowers, fruits or seeds (**13**)] is often brief, these can still affect the aboveground diversity of plant-associated organisms owing to the large active size ranges of aboveground organisms. Large aboveground and belowground organisms might disperse actively in a directional way (**15**), by flying, walking, crawling or burrowing, whereas smaller organisms and seeds disperse more randomly via passive dispersal (**14**) by air, water or via phoresy (**16**) (i.e. using other organisms as transport vectors). Abbreviations: AM fungi, arbuscular mycorrhizal fungi; N-fixers, nitrogen-fixing microorganisms (derived from De Deyn and van der Putten, Trends in Ecology & Evolution, 2005). (GDD, WVDP, JRC) [141]

Drivers of loss

Throughout the past centuries, and especially since the industrial revolution and the production of mineral fertilisers, human impacts on biodiversity have been tremendous and are projected to keep increasing in the coming decades. The main cause of declines in biodiversity is land-use change. Conversion of natural land into agricultural systems in which very few plant species, even very few plant genotypes, are being grown leads to lower soil biodiversity. Awareness of the potential negative effect of this process on ecosystem functions, such as natural pest control, has led to the implementation of alternative cropping systems in which plant diversity is increased through the creation of species- rich field borders, diversified rotations and intercropping.

The scarce large blue (*Maculinea teleius*) butterfly has an intimate relationship with the red ant (*Myrmica scabrinodis*), which takes care of the butterfly's pupae. (ATA, WPP)



Map showing the anthropogenic plant species loss as a percentage of the native plant species richness, including the area of native habitat lost to agriculture and settlements (derived from Ellis *et al.*, PLOS ONE, 2012). (LJ, JRC) [143]

Specialists vs. generalists

The differences between the various species of soil organisms in their response to the decline of aboveground diversity can be explained by the level of dependence on a very narrow or broad range of aboveground species. Specialist species have a narrow range of species on which they can prey, while generalists have a broad range and can easily switch food sources depending on what is available. High levels of specialism are most notable in organisms that coevolved with each other, meaning that they are adapted to specific characteristics. Two notable examples are orchids and their specialist orchid mycorrhizal fungi (see page 40), and blue butterfly species, whose caterpillars are hosted by ants (see page 54) in their nests in the soil; there, the caterpillars are provided with food and protection until the butterfly forms.

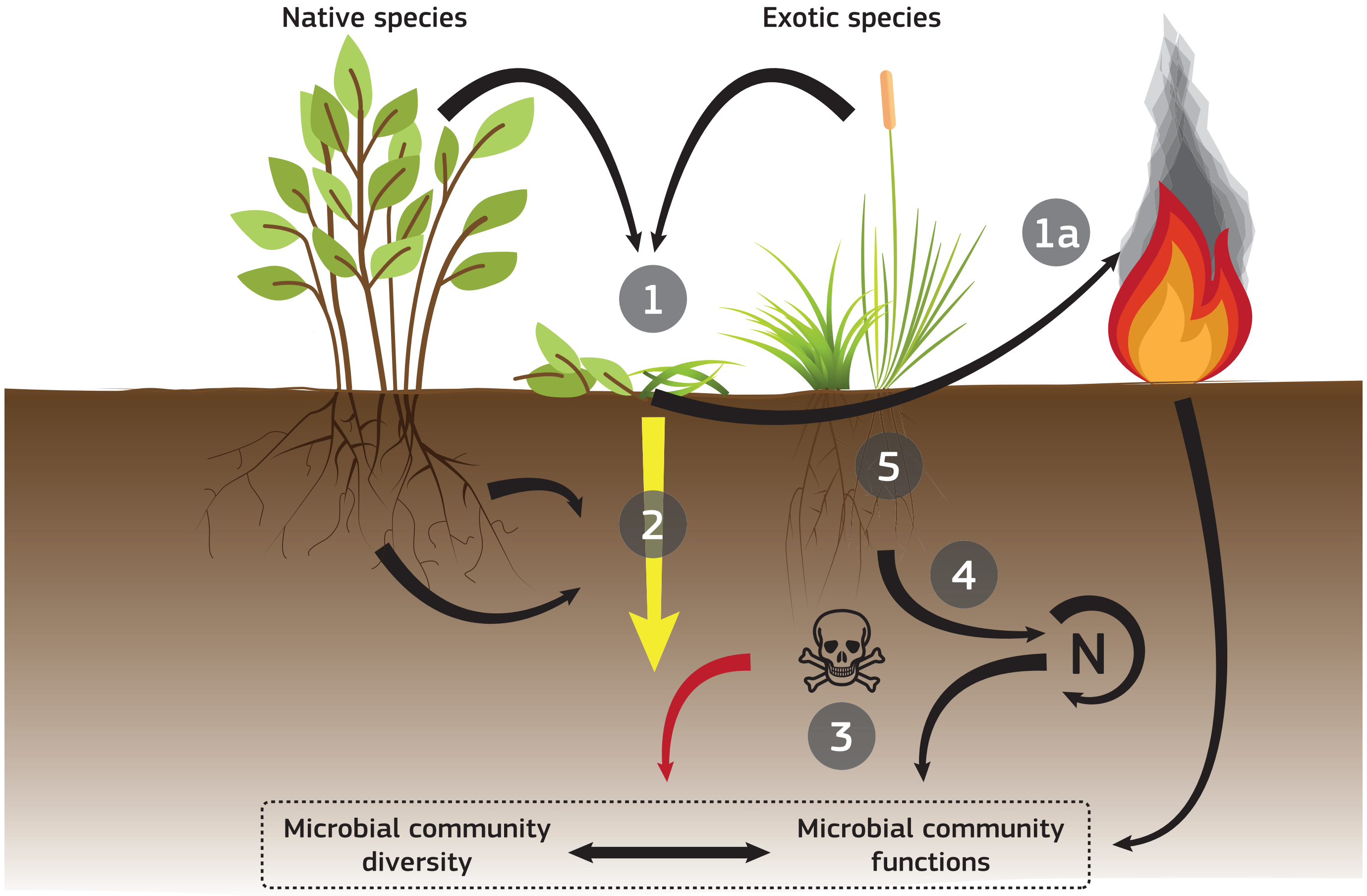
Introduction of invasive species

Invasive species: a global issue

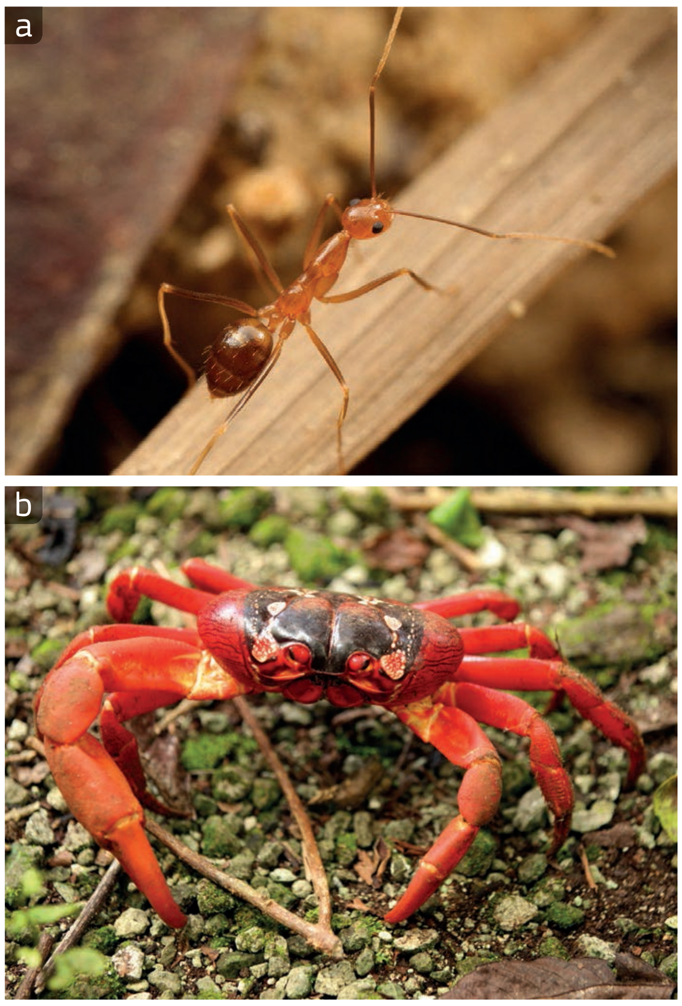
In natural ecosystems, species have evolved together in such a way that generally no single group completely dominates the system and, therefore, they can coexist. When an exotic species arrives or is introduced into an ecosystem, it is possible that it establishes and spreads so profusely that the native species completely disappear because they are being outcompeted. This rapid spread of exotic species is known as an invasion. The organisms that become invasive can belong to any trophic group, such as plants, mammals, invertebrates or fungal species. The impacts of these invasive species are not only notable aboveground; they also directly impact belowground diversity and processes (e.g. when the invasive species lives belowground) or indirectly through changes in plant species inputs into the soil. Over time, an ecosystem that has been overrun with invasive species becomes more and more difficult to restore, as the actual habitat may be altered in such a way as to favour the invasive species. [144]

Invasion risk

The risk of invasion increases with the increase of introduction events. Throughout the last century these potential introduction events have increased tremendously because of greater human trade and mobility. At a global scale it is well recognised that invasive species pose a threat to global species diversity and that invasive species can create substantial economic losses. The Global Invasive Species Database, which is managed by the Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN) Species Survival Commission, keeps track of which species are invasive, and which are becoming invasive, at a global scale.



Simplified illustration of the impact mechanisms of invasive exotic plants on ecosystems and soil biodiversity: (**1**) litter production, (**1a**) inflammability, (**2**) release of molecules from roots (root exudation), (**3**) production of substances with detrimental effects on target organisms (allelopathy), (**4**) new nutrient acquisition strategy (nitrogen fixation and mycorrhiza), (**5**) changes in root architecture or rooting patterns (derived from Wolfe and Klironomos, BioScience, 2005). [144]



(**a**) The yellow crazy ant (*Anoplolepis gracilipes*) introduced accidentally to northern Australia and Christmas Island in the Indian Ocean. (**b**) The Christmas Island red crab (*Gecarcoidea natalis*) is preyed on by the yellow crazy ants. This has had a great impact on the island's vegetation. (SSH, DIBP)

Among the 100 worst invasive species globally there are not only plant species but also several ant species (see page 54), (soil-borne) fungal pathogens (see box on page 39), and soil-dwelling flatworm species. The ecosystems most prone to severe impacts of invasive species are those that have been isolated for a very long time, such as islands, because their native species can be very different from the exotic species.

A striking example is the invasion of the yellow crazy ants (*Anoplolepis gracilipes*) on Christmas Island in Southeast Asia, which led to dramatic ecosystem changes. The indigenous red crab (*Gecarcoidea natalis*) is a key ecosystem engineer on Christmas Island whose feeding and burrowing activities determine the vegetation composition through its impact on the litter layer and plant regeneration.

The yellow crazy ants are very numerous and prey on the crabs until elimination, which results in complete shifts in the vegetation. Moreover, the yellow crazy ants also prey on small isopods, myriapods, molluscs, arachnids, land crabs, earthworms and insects, thereby also directly impacting soil biodiversity and concomitant ecosystem functions.

Impacts of invasive plant species

Of all types of invasive organisms, the invasion of plant species might be best well known by the general public especially when the invasive species cause direct nuisance to human health, such as by causing allergies (e.g. Ragweed pollen, Giant Hogweed skin irritations). For example, the Latin American tree *Prosopis juliflora* has become invasive in semi-arid locations of Africa thanks to its tolerance of high temperatures, drought and salinity stress, its production of specific organic substances that are toxic to native plants (i.e. allelopathic effect), and its hosting of soil-borne native nitrogen-fixing bacteria (see page 105) in root nodules that can resume nitrogen fixation once conditions improve.

Less well known is the fact that invasive plant species can also have far reaching impacts on the species composition and functioning of whole ecosystems through plant-soil feedbacks that modify soil biology, chemistry and structure. The increase in soil organic carbon, nutrients and root biomass (of the invasive plant species) creates an environment that can support a large number of soil organisms, which, in turn, further promote the establishment of the invasive species. The biodiversity of these soils often increases significantly; however, the variety of organisms present also differs significantly from those found in the natural stands, once again limiting the growth of indigenous species.

In a recent study carried out in the Amazon Basin, it was shown that conversion of natural rainforest to pastures (with a relatively homogeneous plant cover) also results in more homogeneous biotic communities, meaning that communities become more similar. Similarly, it has been shown that plant invasions also promote the homogenisation of ecosystems as a whole, with a decline in the diversity of plants.

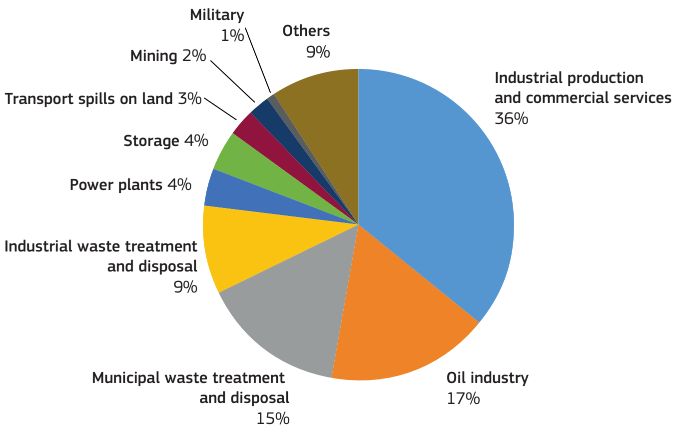
Invasive organisms can radically transform ecosystems when they introduce novel traits into the ecosystem itself. For example, (**a**) waterlogging and vegetation change in the UK resulting from the removal of earthworms by the invasive predators (**b**) New Zealand flatworm (*Aryhurdendyus triangulata*). (**c**) The burrowing earthworm *Lumbricus terrestris* causes the development of a dense understory in sugar maple (*Acer saccharum*) forests in the USA. (KDA, SRA, RHI)

Pollution

Types of pollutants

Soil is an extremely complex environment, which provides soil organisms with food, water, air and shelter. Because of its properties, pollutants that end up on top of or in the soil, can have very strong immediate and long-lasting effects on soil biodiversity. The most common types of soil pollutants are oil, pesticides (see page 123), heavy metals and very high concentrations of salts and fertilisers, caused primarily by industry and municipal waste. [145]

Often the term 'pollution' is confused with the term 'contamination'. Pollution can be defined as the introduction by humans, directly or indirectly, of substances or energy into the environment resulting in deleterious effects on living resources, hazards to human health and restrictions to human activities, including farming. Contamination, by contrast, is the presence of concentrations of harmful substances above the natural background level for the considered environment and the organisms living in it. A large range of pollutants can reach the soil of both natural and modified ecosystems through various routes (direct application, atmospheric fall out, waste disposal, etc.) and influence the functioning of soils on a wide spatio-temporal scale, from individual organisms to landscapes.



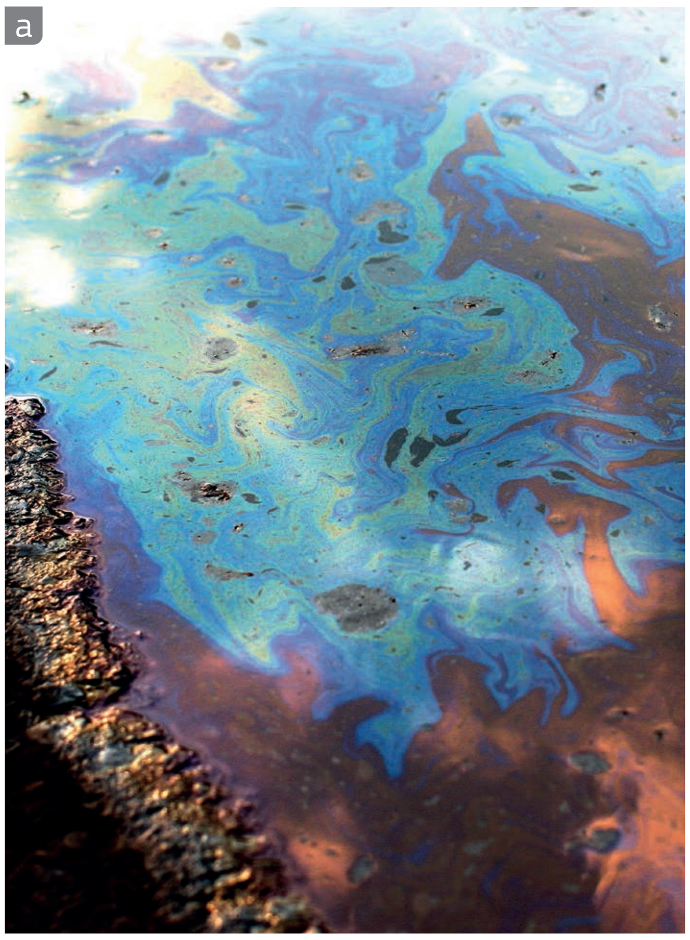
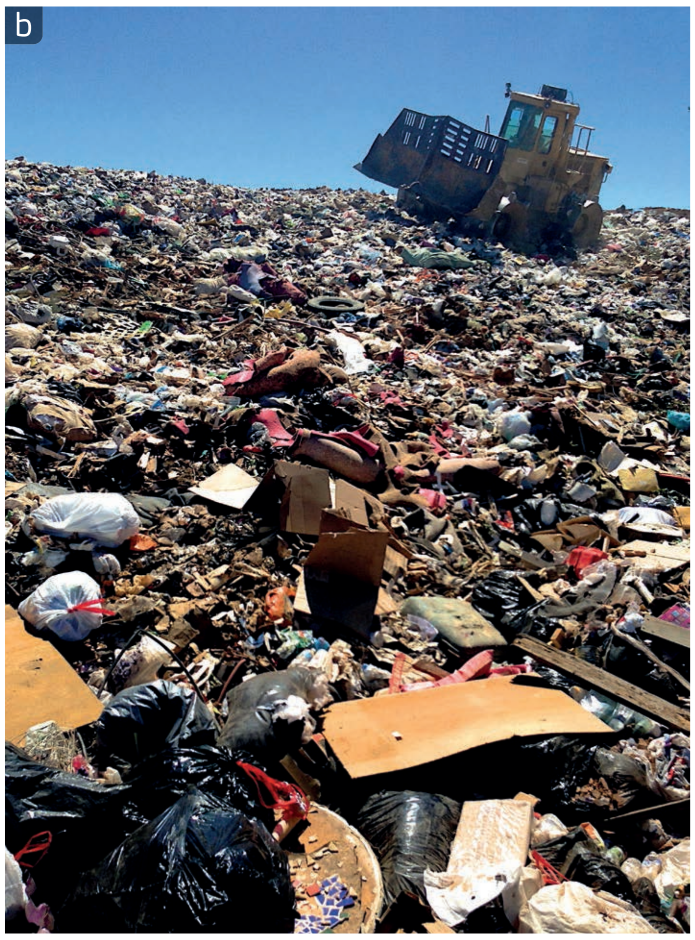
Main causes of soil pollution from human activities. (EEA, JRC)

Effects on soil biodiversity

The impact of pollution on soil biodiversity depends on the type of pollutant and the way it acts on the soil organisms. Oil spills that create a film on the soil block gas exchanges such that it creates a lack of air and suffocates the soil biota in a non-selective way. Pesticides, by contrast, are more selective, killing specific groups of soil organisms as a side effect of their main targets of plant pathogens and pests. For example, insecticides kill insects (e.g. ants and termites – see pages 54-55), nematicides kill nematodes (see pages 46-47), fungicides kill fungi (see pages 38-41), bactericides kill bacteria (see pages 33-35) and acaricides kill mites (see page 49). The level of direct toxicity is often dose dependent. It is important to note that soil organisms can develop resistance to pesticides, especially if their starting populations are large, their rate of reproduction is high and their method of overcoming pesticide activity requires few adaptations (e.g. production of proteins that can detoxify a simple chemical compound).

Heavy metals (e.g. zinc, lead, mercury and cadmium) interfere with the normal metabolism of plants and soil organisms, resulting in lethal physiological and neurological disorders. The very specific impact depends on the heavy metal in question and its availability (i.e. mobility in the soil system). Apart from mining, landfills and industrial sites are also potential hotspots for heavy metal pollution in the soil. Regulations on the type of waste that ends up in landfills and the recycling of waste to reuse the heavy metals are therefore of major importance.

In conclusion, whatever the pollutant, it is important to consider that the impacts on soil biodiversity do not only act via direct toxicity, which either instantly kills soil biota or leads to its reproductive failure, but also have indirect effects on non-target organisms. As soil organisms are dependent on each other through feeding relations, the alteration of any of the components of the food web (see page 96) can impact the rest of the chain. For example, when plant growth is not possible due to high concentrations of pollutants, the abundance of the soil organisms declines because of their dependency on the plant-derived organic matter (see page 106).


Some of the main causes of soil pollution are (**a**) oil spills, (**b**) landfills with municipal waste and (**c**) mining. These practices usually have negative impacts on soil biodiversity. (TOR, ALE, ATH)

Earthworms and pollutants

- Earthworms, contrary to ants and termites which tend to be more resistant to several pollutants, are often highly sensitive to soil pollution.
- Their sensitivity is due both to:
  - close contact with pore water and their highly water-permeable epidermis: water soluble pollutants can easily penetrate into their bodies;
  - the fact that they ingest large quantities of soil.
- Earthworms are able to eliminate excess heavy metals from their bodies, thanks to a physiological control mechanism. Depending on the pollutant, this elimination pathway can be more or less efficient.
- Copper and zinc are easily eliminated by physiological pathways based on carrier systems, which earthworms naturally have for the control of these elements.
- The mechanism of metal detoxification is much slower for cadmium and lead. It involves complex metabolic pathways, including the formation of waste nodules (known as brown bodies). These are aggregated dark-coloured masses usually found in the coelomic cavity at the posterior end of the body and represent the immune system of earthworms.

Earthworms are more sensitive to soil pollutants than other soil organisms, such as ants and termites. As a predator of earthworms, the presence of molehills is an indicator of unpolluted soil. (SCO)

Acid rain and nutrient overloading

Acid rain

'Acid rain' is a broad term that refers to a mixture of wet and dry deposition (deposited material) from the atmosphere containing higher than normal amounts of nitric and sulphuric acids. The precursors of acid rain formation result from natural sources, such as volcanoes and decaying vegetation, and human-made sources, primarily emissions of sulphur dioxide and nitrogen oxides that result from fossil fuel combustion. Acid rain occurs when these gases react in the atmosphere with water, oxygen and other chemicals to form various acidic compounds. The result is a mild solution of sulphuric and nitric acid. When sulphur dioxide and nitrogen oxides are released from power plants and other sources, prevailing winds carry these compounds across state and national borders, sometimes hundreds of kilometres. [146]

The damage that results from acidic deposition has been investigated in all groups of soil organisms. Increasing soil acidity can affect microorganisms (e.g. bacteria and fungi – see pages 33-35, 38-41) that break down organic matter into nutrient forms that are then available to plants. In general, a reduction of species diversity is observed in the presence of acid rains; however, common patterns cannot be identified as the effects vary greatly due to the diversity of microbial functional groups. Considering microfauna, the ability of protists to form resistant structures (see pages 36-37) may be an important feature providing shelter from acid stress.

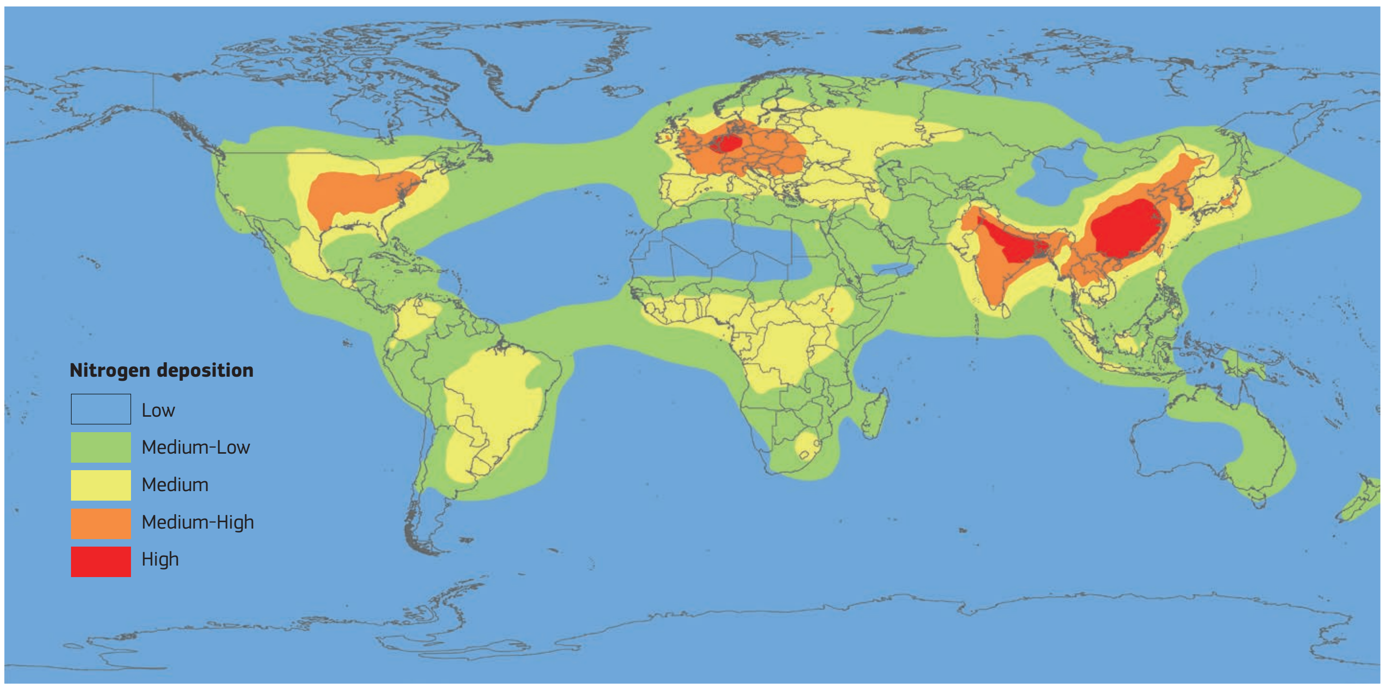
Among the mesofauna, sensitivity to acidity is higher in collembolans and mites (see pages 49-50), whereas many species of enchytraeids (see page 48) are tolerant of acidity. Soil acidification also impacts earthworm communities and their activity (see page 58). In fact, they tend to escape from acidic soils and may eventually die when pH values become too low (pH 2). Furthermore, an inverse relationship between the acidity of the soil and the burrowing rate has been shown; as the environment becomes more acidic (pH 4), earthworms failed to burrow quickly (i.e. under 20 minutes). By contrast, macroarthropods (e.g. coleopterans – see page 59) have a limited susceptibility to low pH values thanks to their hard outer covering (cuticula). However, the high demand for nutrients caused by the development of the cuticula does not allow most of the macroarthropods to survive in an acidified environment.

Acid rain can also have negative effects on plants. Increasing soil acidity allows aluminium (a common constituent of soil minerals) to be solubilised. In its free organic form, aluminium is toxic to plant roots (see page 43) and can lock up phosphate, thereby reducing the concentrations of this important plant nutrient. Nevertheless, under such circumstances it has also been shown that ectomycorrhizal fungi (see page 40) on the roots of some trees help supply much-needed calcium in forest soils subjected to acid rain.

Nutrient overloading

Soils across the globe are receiving nutrient inputs from human activities at rates that exceed those from natural processes. For example, nitrogen (N) inputs to ecosystems are 30-50 % greater now than they were 100 years ago. Similarly, phosphorus (P) inputs via fertiliser applications to agricultural lands are now estimated to be approximately 25 thousand million kg per year, rates that far exceed pre-industrial inputs. These excess amounts of N and P typically enter ecosystems via the direct application of chemical fertilisers or manure to soils in agricultural and pasture soils (see page 88). Alternatively, N and P can enter ecosystems (see page 105), even those largely unaffected by human activities, via atmospheric deposition of phosphorus-containing dust or reactive N oxides. The rates at which N and P have been added to soils has increased dramatically over the past 50 years, with important implications for the structure and function of ecosystems worldwide.

In non-agricultural soils, excess nutrient additions can, over time, lead to significant shifts in plant community composition. Nutrient additions can also lead to changes in soil pH and, in some cases, nutrient toxicity if addition rates are sufficiently high. Moreover, nutrient additions can lead to significant shifts in belowground carbon dynamics, due to changes in the amounts and types of plant-derived organic carbon entering the soil and changes in the rates at which litter and soil organic matter pools are mineralised to carbon dioxide (CO_2) via microbial activities (see pages 102-106).



Map showing estimated nitrogen deposition from nitrogen emissions around the world. Red areas have the highest nitrogen levels and blue areas the lowest (derived from Dentener *et al.*, Global Biogeochemical Cycles, 2006). (JRC) [147]

Nutrient overloading has perhaps the strongest effects on aquatic ecosystems when the soil cannot retain all of the added N and P. The excess nutrients end up in surface and groundwaters, leading to the effect known as eutrophication, which is the excessive growth of algae resulting from high nutrient concentrations.

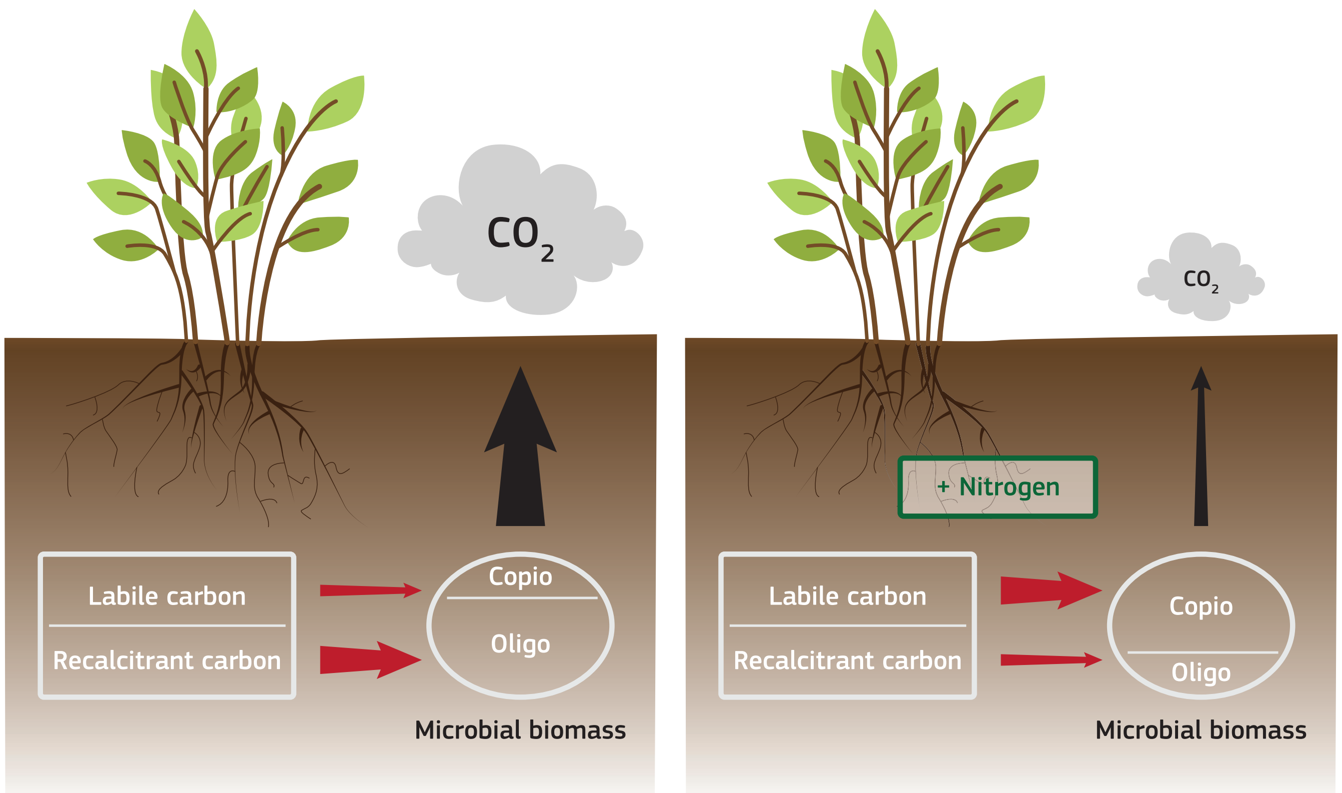
Given the myriad interactions between plants and belowground biota, one of the primary mechanisms through which nutrient amendments influence soil microbial and faunal taxa is by changing plant production and plant community types. For example, nutrient additions often favour the growth of 'weedy' plant species that produce higher quality litter, inhibiting the growth of microbial taxa that specialise in the decomposition of more recalcitrant litter types.

Similarly, mycorrhizal fungal taxa typically become less abundant when soils are amended with nitrogen or phosphorus. The growth of cyanobacterial taxa (see page 35) that are often found on the soil surface in many ecosystems can be inhibited by nutrient overloading due to the increased shading that often accompanies the increased rates of plant growth. Other, more direct effects of nutrient overloading on soil biota include reductions in nitrogen-fixing bacteria and increases in the relative abundances of those taxa that carry out denitrification or nitrification processes (see page 105).

More generally, nutrient additions tend to favour microbial taxa with higher nitrogen and phosphorus demands (which are typically faster growing taxa) and these shifts in bacterial and fungal communities can have cascading effects on the composition of faunal communities and the overall structure of the soil food web.

Changes in soil biodiversity and the functional abilities of these communities that result from elevated inputs of nutrients can have dramatic impacts on the soil carbon cycle (see page 104). For example, it is commonly observed that microbial decomposition of soil organic matter stocks typically drops when soils are amended with nitrogen along with a corresponding drop in the size of the soil microbial biomass pool. However, these responses are not observed across all sites, and nutrient additions can have different effects on litter decomposition (see page 106) when compared to the decomposition of soil organic matter. The decrease in microbial CO_2 production and microbial biomass has been observed in both field and experimental studies across a broad range of soil types, thus suggesting that these responses are nearly universal. However, the mechanisms associated with these nutrient effects on belowground systems remain undetermined.

Decreases in the quality or quantity of plant carbon inputs could contribute to the observed reductions in belowground CO_2 production and microbial biomass with nutrient additions. There also seem to be more direct effects of nutrient additions on microbial communities, whereby nutrient additions decrease microbial decomposition of more recalcitrant carbon pools through the direct inhibition of extracellular enzyme activities or shifts from a more oligotrophic community to one dominated by more copiotrophic (faster growing) taxa. Regardless of the mechanism (or mechanisms) involved, an improved understanding of how nutrients affect the activities of belowground communities is important given that microbial mineralisation of soil organic matter pools is a key component of the global carbon cycle and a key determinant of soil fertility over longer time scales.



Conceptual diagram indicating how nitrogen additions can shift a nutrient-limited belowground community, on the left, to the one on the right with a smaller microbial biomass pool and less soil CO_2 production, by shifting the ratio of copiotrophic (organisms that tend to be found in nutrient-rich environments) to oligotrophic (organisms that can live in a nutrient-poor environment) microbial taxa. (KSR)

Agricultural practices

Low vs. high inputs

Agricultural activities represent one of the most intensive forms of land use, and their impacts on soil biota can be highly variable as a function of the management options adopted. For example, observations on the impact of agricultural management on soil microarthropod communities (e.g. collembolans – see page 50) show that the high input of intensively managed systems tends to promote a reduction in diversity, while lower input systems conserve diversity. High-input systems favour bacterial pathways of decomposition, dominated by labile substrates and opportunistic bacterial-feeding fauna (e.g. nematodes – see pages 46-47). By contrast, low-input systems favour fungal pathways with a more heterogeneous habitat and resource dominated by persistent fungal-feeding fauna (e.g. termites – see pages 55). [148]

Demand for agricultural crops is expected to double as the world's population is expected to reach 9 thousand million by 2050. Increasing the quantity and quality of food in response to growing demand will require increased agricultural productivity and improvement of agricultural practices. (DDA)

Soil tillage

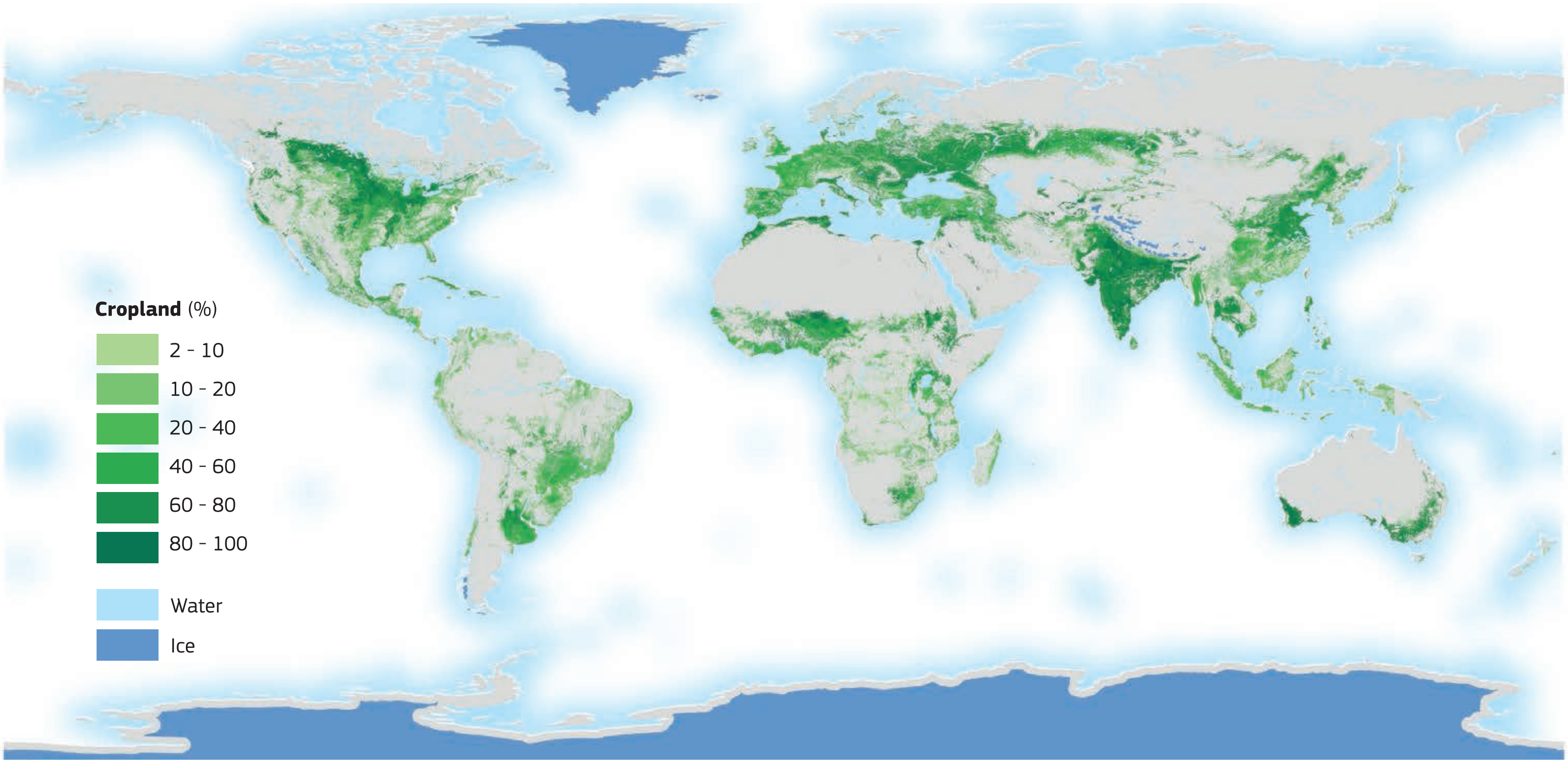
Soil tillage causes significant modifications in the soil, especially with regard to soil structure, porosity and water-holding capacity, but also organic carbon content. The impact of tillage on soil organisms is highly variable, depending on the tillage system and soil characteristics.

Three main tillage systems are recognised: conventional, minimum and no-till. Conventional (intensive) tillage (i.e. ploughing) inverts and breaks up the soil, destroys the soil structure and buries crop residues, causing the most significant impact on soil organisms. Minimum tillage systems can be characterised by a reduced tillage area (i.e. strip tillage) and/or reduced tillage depth (i.e. by using a rotary tiller, harrow and hoe); crop residues are generally incorporated into the soil instead of being buried. Under no-till conditions (see pages 146-147), the soil remains relatively undisturbed and plant litter remains on the soil surface, similar to natural soil systems, providing a more stable habitat.

As conventional tillage tends to favour bacteria (see pages 33-35), it would also be expected to favour protists (see pages 36-37), since bacteria are their main food source. Total nematode numbers have been found to either increase or decrease with tillage. Their wide range of responses probably reflects the wide range of functional groups and trophic levels (i.e. fungivores, bacterivores, omnivores, predators and plant parasites – see pages 46-47). Considering soil meso- and macrofauna, tilled systems generally host organisms with a short generation time, small body size, rapid dispersal and omnivorous feeding habits. Collembolans (see page 50) are usually inhibited by tillage disturbances, although some studies have shown the opposite effect. Mites (see page 49) exhibit a wider range and more extreme responses. Tillage is also one of the most detrimental factors for earthworm communities in agricultural soils. It disturbs and destroys their habitat, and physically damages them through the plough blades and inversion tillage. The earthworms are moved to the surface where they are exposed to bird predation. The specific effect of tillage on earthworms depends on the type of tillage, and on the earthworm species or functional group (see page 58).

Soil tillage also influences the sensitivity to compaction, which in turn impacts soil biota. Conventionally tilled soils have lower bearing capacity and, consequently, are more sensitive to compaction caused by agricultural machinery. Considering soil organisms, lower earthworm populations are found in fields with more tractor traffic. The abundance of microarthropods generally decreases with increasing soil compaction, with collembolans being more sensitive than mites to this kind of pressure.

Soil ploughing is still one of the most common tillage practices, often resulting in a reduction of soil biodiversity. (BTU)



Map showing global cropland cover for the baseline year 2005. It has been developed using a bottom-up approach: integration of existing maps shared by the community, and the development and validation of products driven by crowdsourcing through the availability of very high-resolution satellite imagery. For crowdsourcing, the Geo-Wiki Platform (www.geo-wiki.org) was used. Geo-Wiki is a platform that provides citizens with the means to engage in environmental monitoring. In this case, land cover information was gathered for the validation of the map. The map has a resolution of 1 km^2 (derived from Fritz *et al.*, Global Change Biology, 2015). (LJ, JRC) [149]

Fertiliser applications

Fertilisers are often applied in agriculture to maintain high yields. Two main types of fertilisers can be used: organic and inorganic. Organic fertiliser consists of materials that come from different types of organisms. Organic fertilisers, such as crop residues or animal manure, serve as an extra food source for the soil decomposer community (see page 106) and often increase their population density and biomass. Inorganic (mineral) fertilisers are sometimes completely, or at least partially, comprised of man-made materials. Inorganic fertilisers do not directly serve as a food source for soil organisms. However, by increasing crop growth, they make more organic matter (roots or plant residues) available after the harvest and, therefore, may have indirect effects on soil biota.

Several studies demonstrate that the total soil microbial biomass and the biomass of many specific groups of soil organisms reflects the level of soil organic matter inputs. Therefore, organic or traditional farming practices that include regular inputs of organic matter in their rotation, generally have larger soil communities than conventional farming practices. For example, solid manure has a positive effect on soil organisms, especially on earthworms (see page 58).

Inorganic fertilisers were reported to have variable impacts on soil organisms. For example, several studies show that high levels of nitrogen inputs are associated with a decrease in species richness and abundance of microarthropods. Mineral fertilisers can also impact earthworms by reducing their abundance; the mechanism can be associated with the soil acidification effect of nitrogen from the mineral fertilisers.

Pesticide applications

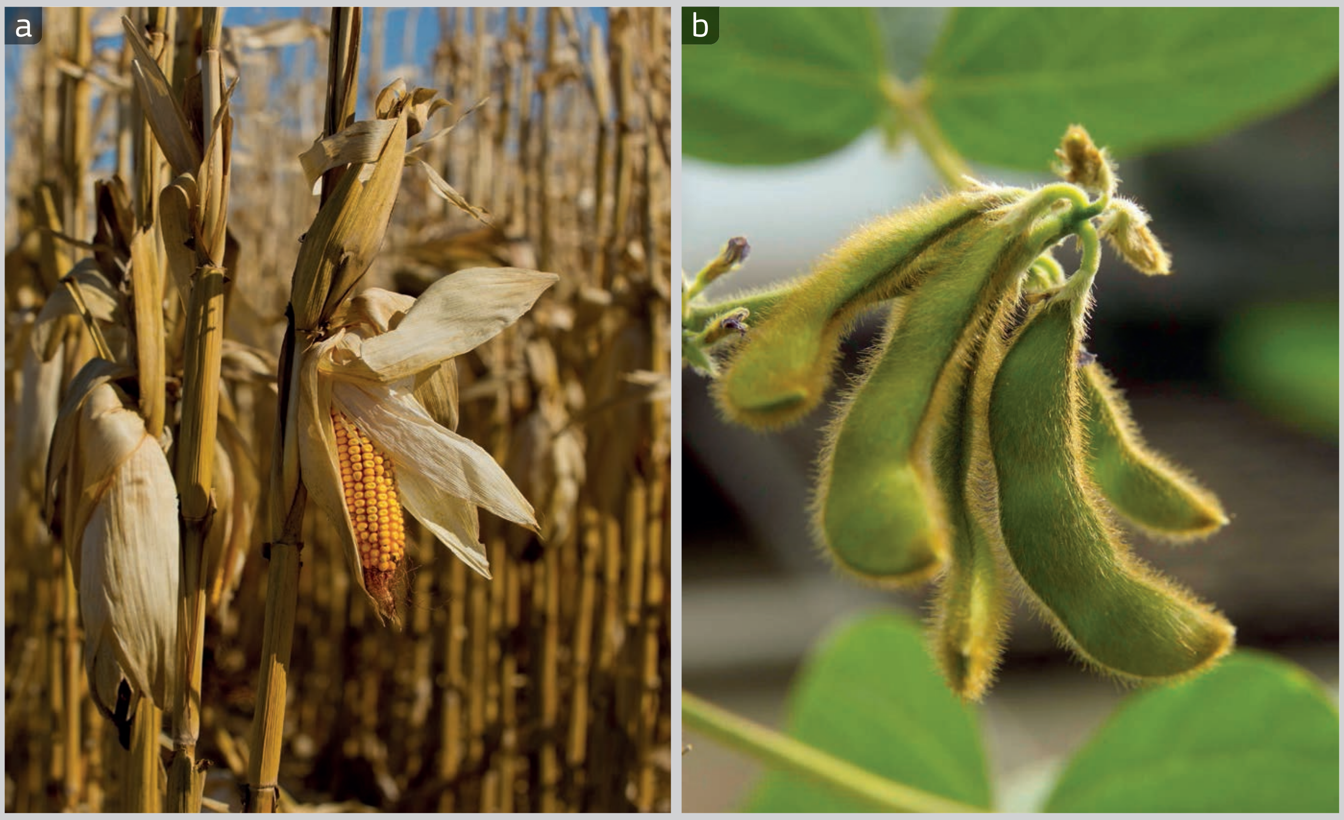
A pesticide is any substance or mixture of substances aimed at preventing, destroying or mitigating pests. It goes without saying that pesticides are detrimental to their target organisms, but non-target organisms can also be unintentionally negatively affected. Pesticide application to the soil can affect soil communities by influencing the individuals' performance and modifying ecological interactions among species. When one or more soil-living species are impacted by a pesticide, this can affect the whole soil food web in terms of abundance and composition.

Pesticide toxicity mainly damages soil fauna. The impact is determined by different factors, such as chemical and physical characteristics, species sensitivity and soil type. For example, among soil microarthropods, different taxa have a variety of responses depending on the substance applied. A laboratory study comparing the responses of soil microarthropods to five insecticides allowed for the toxicity ranking of these products and identification of the main non-target collembolans and mites (see pages 49-50) affected. Several studies found negative effects of various pesticides on earthworm abundance. Generally the negative effects increase with increased dosages of a pesticide. Because of this sensitivity to chemical substances, earthworms are widely used as bioindicators of soil quality and level of soil pollution (see page 101).

The application of fertilisers and pesticides is used to promote plant growth and facilitate harvest, but can have a negative impact on soil biodiversity. (SUS)

Genetically modified organisms and soil biodiversity

- A genetically modified organism (GMO) is an organism whose genetic material has been modified (see page 100). GM crops are used in agriculture, the main crops being: maize, soybean, cotton and canola. The global cover of GM crops reached 175 million hectares in 2013. Pesticide-resistant GM crops represent approximately 80 % of total GM crops. Insect-resistant GM crops, such as Bt maize and Bt cotton, that contain genes from the bacterium *Bacillus turingensis* (Bt), represent 20 %. [150]
- Besides the benefits offered by GM crops, such as a reduced use of pesticides, there is concern about the potential negative effects of GMOs on the environment. One of the largest uncertainties is the effect of GM crops on non-target organisms, such as several soil-living species.
- Only limited research has been carried out on the effects of GM crops on non-target soil organisms. In a short-term experiment with the earthworm *Lumbricus terrestris* in soils containing Bt maize residues, or where Bt maize was grown, Bt toxins were found in the gut of earthworms, but there was no reduction of body weight or increased mortality. Other studies showed the persistence of Bt toxins over the whole cropping season (200 days) – and a decrease in body weight of *L. terrestris* by 18 %.
- Contrasting results were found in an assessment of the impact of GM crops on arbuscular mycorrhizal fungi. A study showed no consistent differences between AM fungal communities associated with GM and non-GM plants. Another study observed a reduction in AMF colonisation in Bt maize. These results show the current need to further investigate the impacts of GM crops on soil biota.



(**a**) Maize and (**b**) soybean are among the most cultivated GM crops. In 2013, 27 countries worldwide planted GM crops. (USB)

The physical and chemical characteristics of soil (see Chapter I), such as texture, structure, pH and organic matter content, also determine the toxic effects of pesticides. For example, it has been shown that the smaller the particles a soil is composed of, the longer a pesticide persists in it.

Pesticide application does not always have negative effects on the soil community. For example, for certain types of soil there is evidence that some taxa can obtain a competitive advantage from the application of certain specific pesticides due to the elimination or reduction of their competitors from the environment.

Monoculture

Another agricultural practice relevant to soil biodiversity is related to the diversity of crops. Monoculture is the agricultural practice of growing only one crop or plant species at a time. Polyculture, by contrast, where more than one crop is grown at the same time, and crop rotation, where different plant species are grown year after year, are the alternatives to monoculture. Monocultural cropping is a very common practice in industrial agriculture and has allowed for increased efficiencies in planting and harvesting. Continuous monoculture, or monocropping, where the same species is grown year after year, can lead to a buildup of pests and diseases and, consequently, their rapid spread where a uniform crop is susceptible to a pathogen. Therefore, monocultures usually require high inputs of pesticides.

Due to the strong links between above- and belowground communities (see page 118), monocultures can impact soil-living organisms. For example, bacterial communities of soils under monocultures in the Argentinean Pampas are less diverse than those in the same soils under crop rotations. Mesofauna, mite and collembolan communities in a natural forest and a spruce monoculture in the Czech Republic were found to be diverse not only in terms of density – mites and collembolans are more abundant in the natural forest – but also in terms of structure. In particular, in the spruce monoculture, groups susceptible to disturbance are suppressed.

Similarly, partially soil-living (hemiedaphic) collembolans increase in the monoculture at the expense of soil-living (edaphic) species. In Canada, earthworm density was greater in a polycultural system that combined crops with trees than in a conventional agricultural monoculture. This is likely because the trees deposit leaf litter which is incorporated into the soil and increases soil water content, thus promoting earthworm presence.

The presented case studies demonstrate how the reduction in variety of food sources and elimination of micro habitats caused by monocultures are a serious threat to soil communities.

Monoculture is the practice of producing or growing crops singly over an area of land. This practice has negative effects on the whole soil community, from microorganisms to earthworms. (RWI)

Overgrazing

Large grazers vs. grasslands

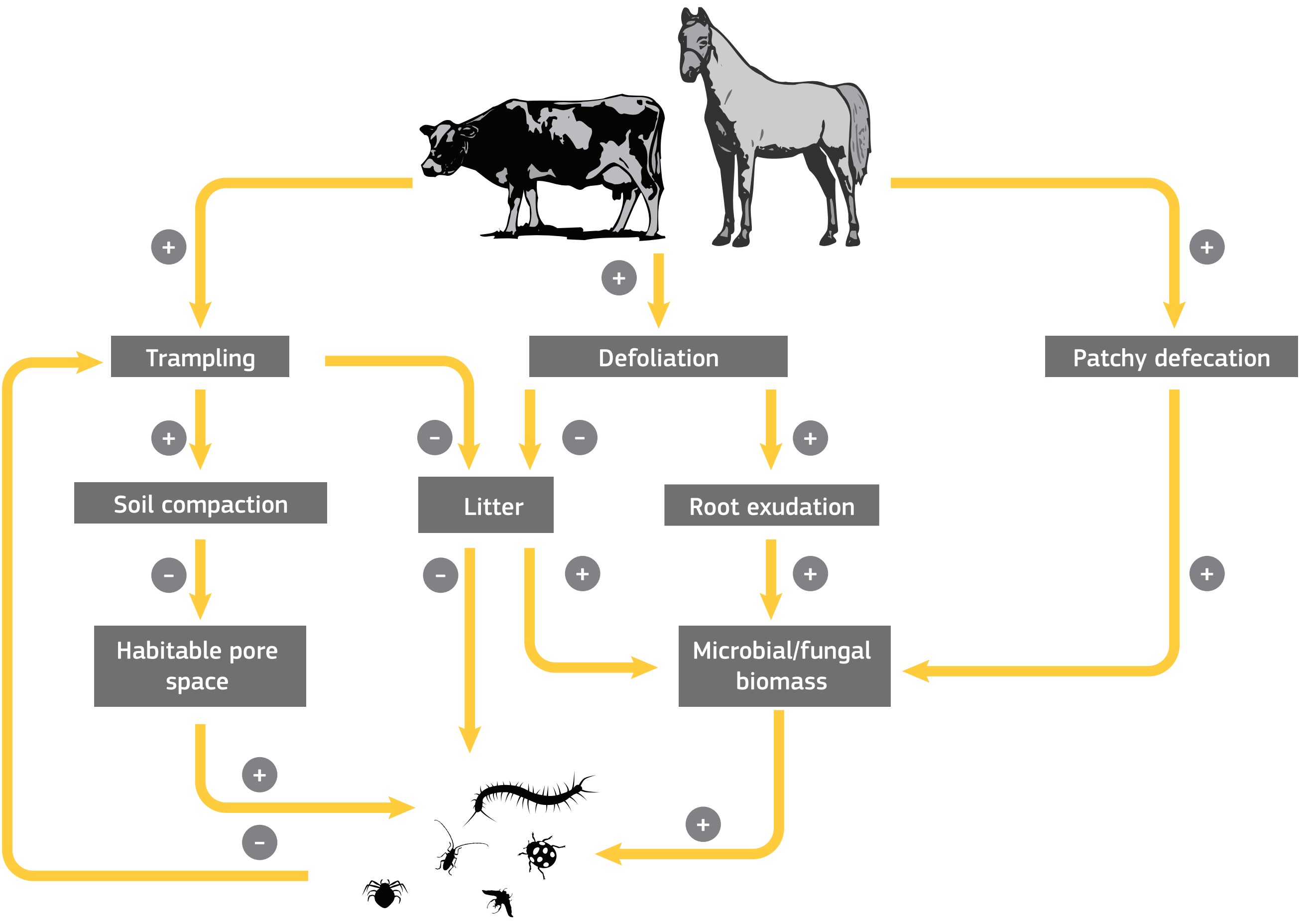
Worldwide, grasslands (see page 81) comprise roughly 40 % of the terrestrial surface. Only a small part of these grasslands can be considered 'natural', meaning that in the absence of grazing these grasslands would turn into shrub and, subsequently, forest. A large proportion is used by humans for livestock grazing. These are often located on marginal soils, where arable farming is not possible because of nutrient deficiency or lack of or excess water.

Grazing by large mammals can have both positive and negative effects on soil organisms and, because these processes occur simultaneously, the overall outcome for soil biodiversity will depend on the stocking density of the large grazers. With increasing densities, the negative effects (e.g. trampling, soil compaction, denudation, resource competition, reduction of shelter, and in many cases antihelminthic residue in faeces), will soon overshadow the positive effects (e.g. increased root exudation, nutrient return through defecation). When exactly this tipping point is reached is difficult to determine, and is likely to vary with ecosystem type, geographic location and land-use history. [151]

Overgrazing can be defined as the practice of placing too many livestock for too long on the same piece of land, or of grazing ruminants on land unsuitable for grazing (i.e. due to certain physical parameters, such as slope). (DRO)

Grazing at high stocking densities, and especially overgrazing, is probably the largest threat to soil biodiversity in grassland systems. This threat can be expected to increase, which is likely to happen in areas with human population growth. What is considered high or low stocking densities is, however, highly dependent on ecosystem productivity (in terms of water and nutrient availability), grazing system (year-round, seasonal or rotational grazing) or soil type. For example, on a highly productive floodplain a density of five sheep per hectare is considered low, whereas this is considered extremely high for a relatively unproductive arctic grassland.

In general, three actions performed by large grazers affect soil biodiversity: defoliation, defecation and trampling. These processes have contrasting effects on soil faunal diversity, through complex direct and indirect interactions with plants, soil microorganisms and soil physical structure.



Conceptual framework of the most important mechanisms through which livestock or other large grazing mammals can affect soil organisms. The arrows represent causal pathways, and the sign (+/–) for each arrow indicates the link between the box in which the arrow starts and the box in which the arrow ends. A pathway from top to bottom with only plus signs (+) indicates general positive effects of large grazers on soil organisms; the minus sign (–) indicates that effects are generally negative. (DVI, JRC)

Defoliation

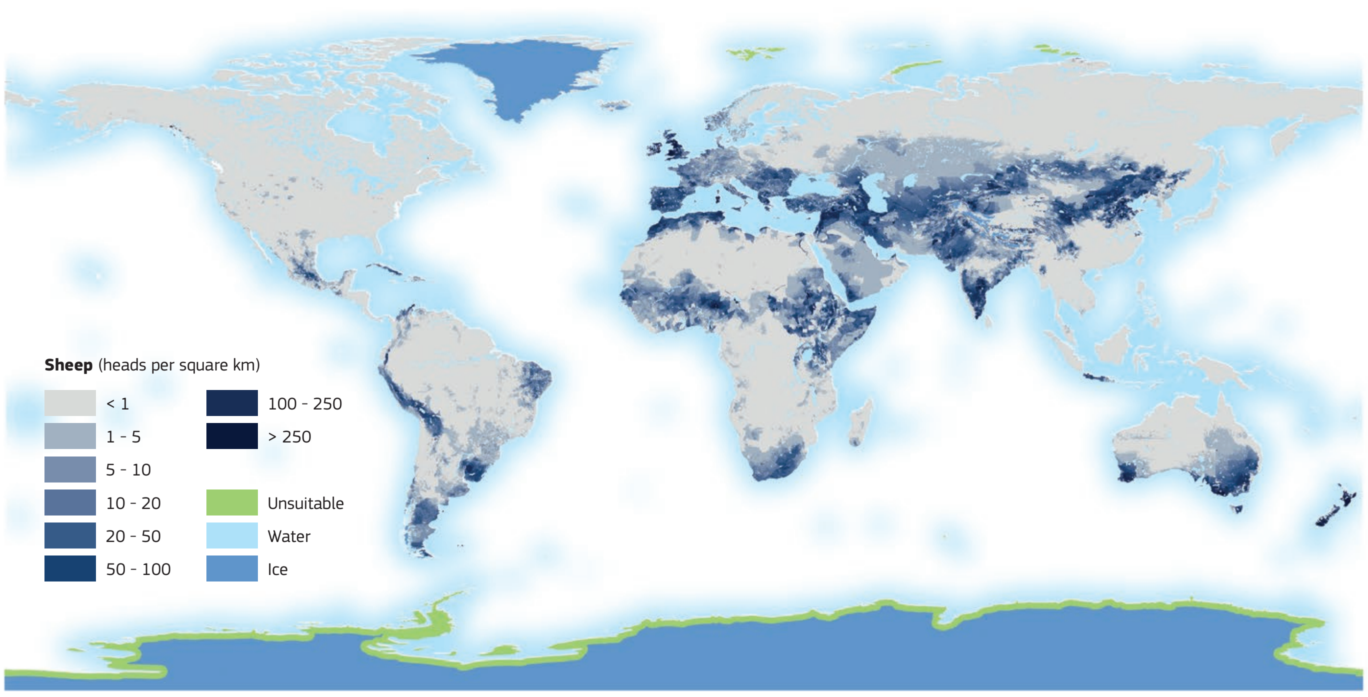
Both large grazers and soil animals depend on plant growth for sustenance. All plant material that is not consumed by large grazers or smaller herbivores will become available to soil invertebrates. Therefore, it can be expected that defoliation (as a result of grazing) takes place at the expense of soil organisms, since they are competing for the same food source. In the short term (hours/days) this is indeed the case: plant material that otherwise would become available to soil animals is consumed by a grazer. However, in the somewhat longer term (days/weeks) grazing can stimulate the activity and abundance of animals in the belowground food web: the network of interactions between soil organisms.

Defoliation forces plants to regrow. In order to do so, they produce sugar-like substances called root exudates that stimulate the growth of microorganisms (e.g. bacteria and fungi – see pages 33-35, 38-41), thus resulting in the release of plant nutrients and an increase in the abundance of soil biota. Defoliation can therefore stimulate plant growth and increase the total amount of available resources for both above- and belowground herbivores.

Moreover, the plant tissue that regrows after defoliation is of much higher quality for herbivorous animals as it is richer in proteins and contains lower amounts of indigestible cell walls. This plant material is also easier for soil organisms to decompose.

Not all organisms profit from defoliation, however. For example, larger-bodied litter fragmenters, such as isopods and millipedes (see pages 56-57), depend on large quantities of poorly degradable plant litter and moist conditions that are present under dense vegetation cover. These often show a pronounced decrease in response to grazing.

Defoliation by (**a**) domesticated and (**b**) wild animals can have negative effects on soil organisms, such as isopods, that require large amounts of leaf litter to survive. (KLA, SOG)



Map of global sheep density in 2006 based on statistical relationships between survey and census data and various variables relating to climate and the environment, and other spatial data relating to demography and land cover (derived from Robinson *et al.*, PLOS ONE, 2014). (LJ, JRC) [152]

Defecation

Patchy deposition of dung and urine (defecation), through which nutrients are returned to the soil, is a second pathway used by large grazers to affect soil organisms. Dung pellets attract a suite of specialised dung-degrading organisms, such as dung beetles, flies and rove beetles (see page 59). These animals are of great importance for the rapid degradation of dung, as well as the redistribution of nutrients through the ecosystem.

Anti-worming agents (anthelmintics), which are routinely administered to most livestock, can have strong negative effects on dung-degrading fauna as well as on the rates of decomposition of the dung pellet. For example, the use of the broad-spectrum antiparasitic Ivermectin results in delayed or reduced growth of beetle larvae and strong reduction in the number of fly larvae. A number of studies have indicated that earthworms (see page 58) are not negatively affected, but cthe reason for this is largely not understood. The use of this drug not only negatively affects nutrient cycling, but may also result in a lower abundance of prey items for grassland-inhabiting birds.

Dung beetle (*Kheper nigroaeneus*) rolls a ball of freshly deposited white rhino dung. (MPV)

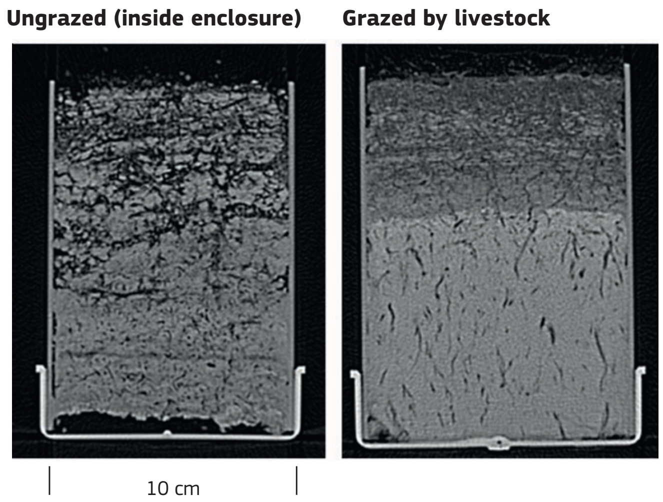
Termites and ants as food

- Mammals feed on termites and ants; in fact, 138 different mammal species eat termites and 180 eat ants.
- They range from antelope to elephant shrews. Some, such as anteaters and pangolins, are also specialised in catching them.
- Termites and ants have developed defence strategies to protect themselves from attack by mammals. Bites by the large mandibles of soldier ants is likely the most well-known method; however, some species also produce chemical substances that distance predators. A less well-known strategy considers a diet based on soil particles that make termites poor in terms of nutritional quality and thus less attractive.
- However, none of these defences prevent mammalian predation. Instead, they limit predation by decreasing the food value of the colony on which the mammals are feeding.

Trampling

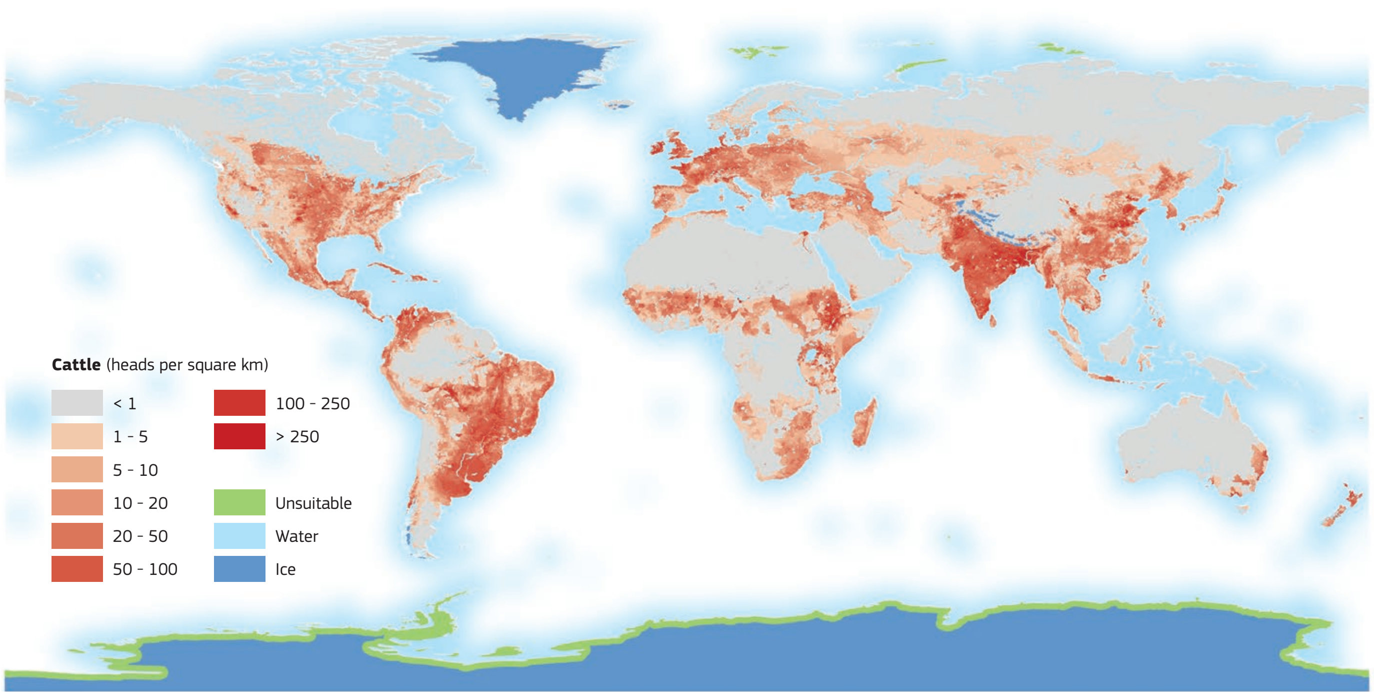
A final major effect that large grazers have on soil organisms is trampling, which can directly affect animals living in the litter layer on, or just under, the soil surface. Indirect effects may be stronger. One indirect effect that trampling can have on soils is denudation, where all vegetation is stripped away from the soil. This usually only happens under high grazer densities.

A second major effect of trampling is the compaction of the soil. Soil organisms inhabit the soil matrix, which consists of pores of various sizes. The largest animals generally live in the largest pores, smaller animals live in smaller pores and the smallest pores are usually only inhabited by bacteria. Trampling by grazing mammals can cause these pores to collapse, with the larger pores collapsing first. Therefore, the largest animals would be expected to face the strongest consequences of trampling. However, many studies show that grazing at low densities is not necessarily detrimental to earthworms. This is probably because earthworms can create their own burrows, thereby shaping a habitat for themselves and other soil organisms. Other animals, and especially soft-bodied soil animals such as collembolans (see page 50), which do not possess this ability, have often been found to be very vulnerable to trampling.

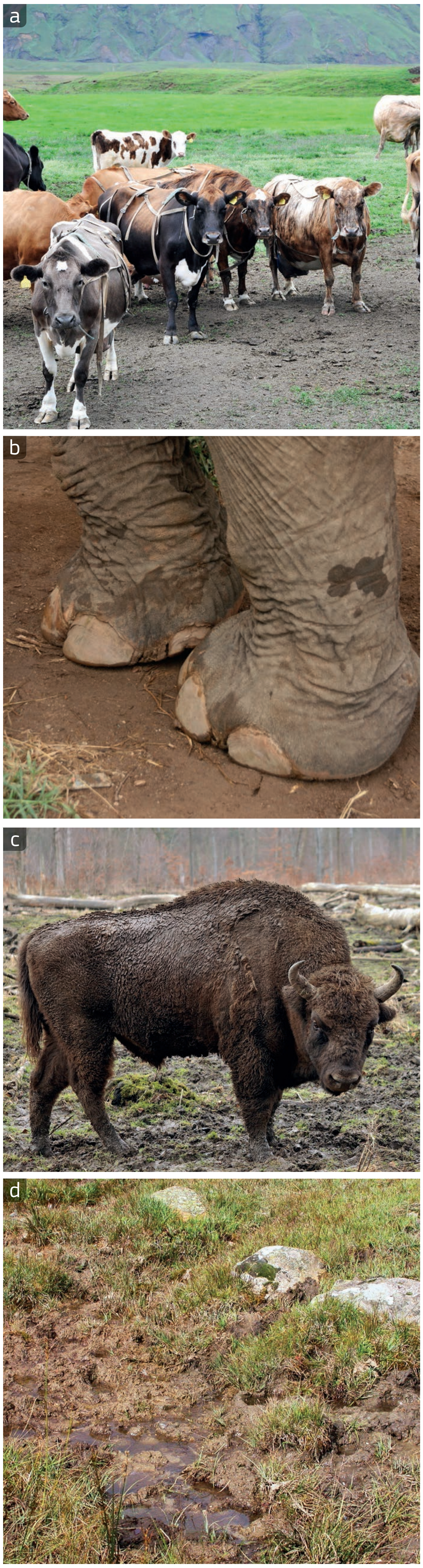


Computed tomography scan of soil cores from ungrazed and grazed temperate salt marshes on clay soil. Dark areas show pore spaces, which are strongly reduced after grazing. (HOL)

The effects of soil compaction are strongest on fine-textured clay and silt soils. The collapse of pore spaces not only affects soil animals directly, but also inhibits the transport of water through the soil. On dry soils, such as the steppes (see page 81) of northern China, soil compaction leads to decreased water penetration. This reduces plant growth and soil biodiversity, and increases superficial runoff and soil erosion (see pages 128-129). By contrast, on very wet soils, such as riverine flood plains and coastal salt marshes, overgrazing of clay soils may result in waterlogged conditions as natural drainage in these soils is blocked. This can result in a decrease in soil oxygen, creating suboptimal conditions for soil fauna and reduced mineralisation rates. In such soils, invertebrate life is often confined to the upper soil layer.



Map of global cattle density in 2006 based on statistical relationships between survey and census data and various variables relating to climate and the environment, and other spatial demography and land-cover data (derived from Robinson *et al.*, PLOS ONE,2014). (LJ, JRC) [152]



Soil compaction is caused not only by livestock, such as (**a**) cattle, but also by wild animals, such as (**b**) elephants and (**c**) bison, living in grasslands. The effects on soil organisms can be both direct and indirect; for example, the resulting soil compaction can (**d**) block water movement, thus affecting soil life. (IVI, KBA, MGA, TWA)

Fire

Fire and human activities

Fire is a natural part of most terrestrial ecosystems. Some ecosystems even came into existence because of fire, such as the savannah (see page 82): fires needed to burn the forests before grasses could establish themselves, only as recent as ~ 50 million years ago (flowering plants appeared ~ 200 million years ago). Fire-exclusion experiments on an Australian savannah showed that, in as little as 20 years, trees can re-establish themselves to such an extent that subsequent fires are not able to kill the trees and bring back the savannah ecosystem. The key factor to consider is the mean fire return interval. The savannah may need a short mean fire return interval of less than 20 - 30 years, but for other ecosystems the balance between burning and recovery periods ranges widely from about 100 to 200 years for temperate forests to > 800 years for peatlands. This natural balance is often disturbed by human activity. Most wildfires nowadays are ignited by humans, through accidents or negligence (e.g. camp fires), side effects of human structures (e.g. sparks from railroads) and, surprisingly commonly, through arson. [153]

Apart from igniting wildfires directly, human activity can also prime ecosystems for burning, making them vulnerable to fire. For example, plantations of fire-prone species such as eucalyptus and pine have replaced less fire-prone vegetation in many parts of the world. Inadequate regulation often means that these plantations cover large uninterrupted areas, allowing fires to spread further than they would in the more fragmented landscapes that they replaced. Peatland draining is perhaps one of the most extreme examples of human activity priming ecosystems for burning. Natural peatlands (see page 25) have relatively high water tables, at commonly 10 - 30 cm depth, which causes the accumulation of organic material from decaying sphagnum moss to depths of one to several metres (at 190-metre depth, the Philippi peatland in Greece is the thickest known peat deposit in the world). To utilise peatlands for agriculture or forestry, people started lowering the water table by installing drains. While under natural conditions a fire would only consume the peatland vegetation, under drained conditions fires can also burn the peat itself, often as smouldering combustion. However, peatlands are sensitive ecosystems, and less severe fires can still have important impacts on soil biodiversity. Considering that peatlands have relatively large numbers of endemic species (i.e. native to that particular area), the impacts of peatland fires on biodiversity may be expected to be disproportionately large.

A (**a**) wildfire changes the ecosystem by (**b**) lowering the soil surface and exposing tree roots anchored in the underlying layers. Such alterations strongly impact the soil-living community, especially that of the litter layer. (LCH/USDA, ARD, USFWS).

Effects on soil biodiversity

The impact of fire on soil biodiversity in grasslands, shrublands and forests (see Chapter III) is primarily dependent on the heat flux into the soil, which, in turn, depends on the fire severity (temperature and duration), the distance to the soil and the soil conditions themselves. For example, although crown fires may be very intense, their distance from the soil limits the heat flux to the soil. The heat from a grass fire may be very high, but it also moves quickly thereby limiting the heat flux into the soil. Surface fires that burn shrubs and forest debris produce a high fire severity with an increased likelihood of the heat flux reaching (further) into the soil. Soil conditions determine how deep the heat flux reaches; for example, drier soil of lower bulk density facilitates the heat flux.

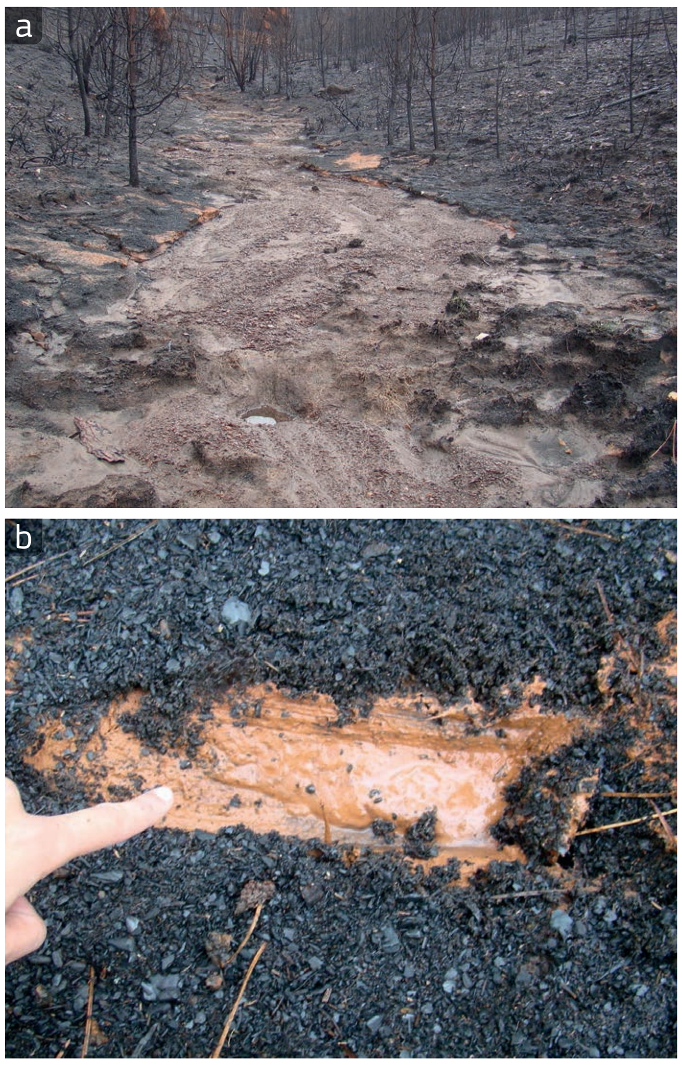
Beetles that inhabit the top layer of soil are among the most vulnerable species to fire. (BDU)

The most vulnerable soil organisms are those that reside in the organic soil layers on top of the soil, such as beetles (see page 59), because the heat flux is strongest there and often the organic soil layers are burnt themselves. Lethal temperatures for soil bacteria (see pages 33-35) range from 50 to 210 °C, while soil fungi (see pages 38-41) are generally more temperature-sensitive than bacteria. Apart from direct effects, the indirect effects of fires on soil biodiversity can be as, or more, important.

The direct effects of fire on soil biology can be severe when there is a large fuel load close to the soil, resulting in a strong heat flux, combined with a low soil moisture content which allows the heat to travel deeper into the soil. In many cases, the direct effects are less severe; otherwise, the soil biology would bounce back from the effects of the heat flux if there were no further disturbances. However, further disturbances after the initial fire event are commonplace and their impacts on soil biota can be as great as, or greater than, the heat flux.

Many soil processes change after a fire, but post-fire soil erosion probably has the greatest impact. Wildfire increases the soil's vulnerability to erosion by removing the vegetative cover that previously protected the soil from the impacts of raindrops, but it can also alter the soil properties themselves, negatively affecting soil structure and thereby increasing the erodibility of the soil.

Wildfire oxidises the organic matter in the soil, leaving behind a structureless soil that will erode very easily. The subsequent loss of soil by erosion (see pages 128-129) can be gradual or dramatic, depending on the intensity and duration of the rainfall, and forms a loss of habitat for soil organisms. In cases where the actual amount of soil lost is relatively small, the loss of soil structure, organic matter and nutrients can still have impacts on soil biology. This means that, apart from the resilience (see page 97) of the pre-fire biological community, colonisation by new species will also occur.



Post-fire soil erosion in a eucalyptus plantation in the Caramulo Mountains of Portugal. (**a**) The process of soil and nutrient loss by post-fire erosion. (**b**) The structureless soil underneath a layer of char produced by the fire. (OGP)

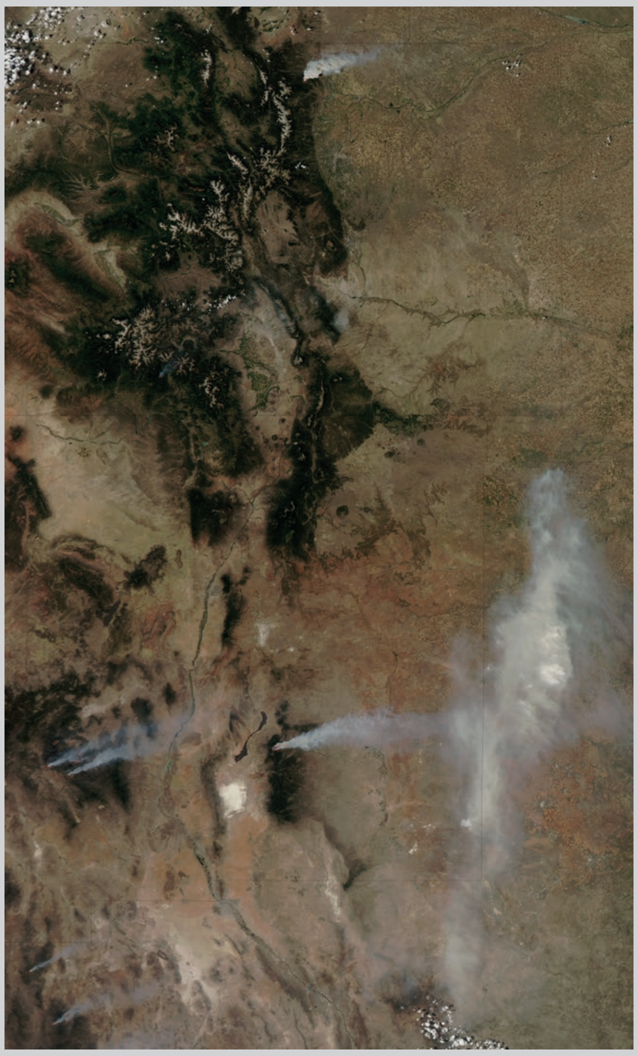
Post-fire land management

Management operations after wildfire can have positive or negative consequences for soil biology. Scientific experiments have shown that forest residue mulching can keep soil erosion within tolerable limits. However, common practices include ploughing and terracing operations. These often increase soil erosion, for example, terracing can sometimes increase soil erodibility by 10 to 100 times tolerable limits. Beyond erosion of the topsoil (see page 10), including soil organisms, the terracing operations completely remove the topsoil, which then gets mixed and diluted into lower soil horizons of the terraces.

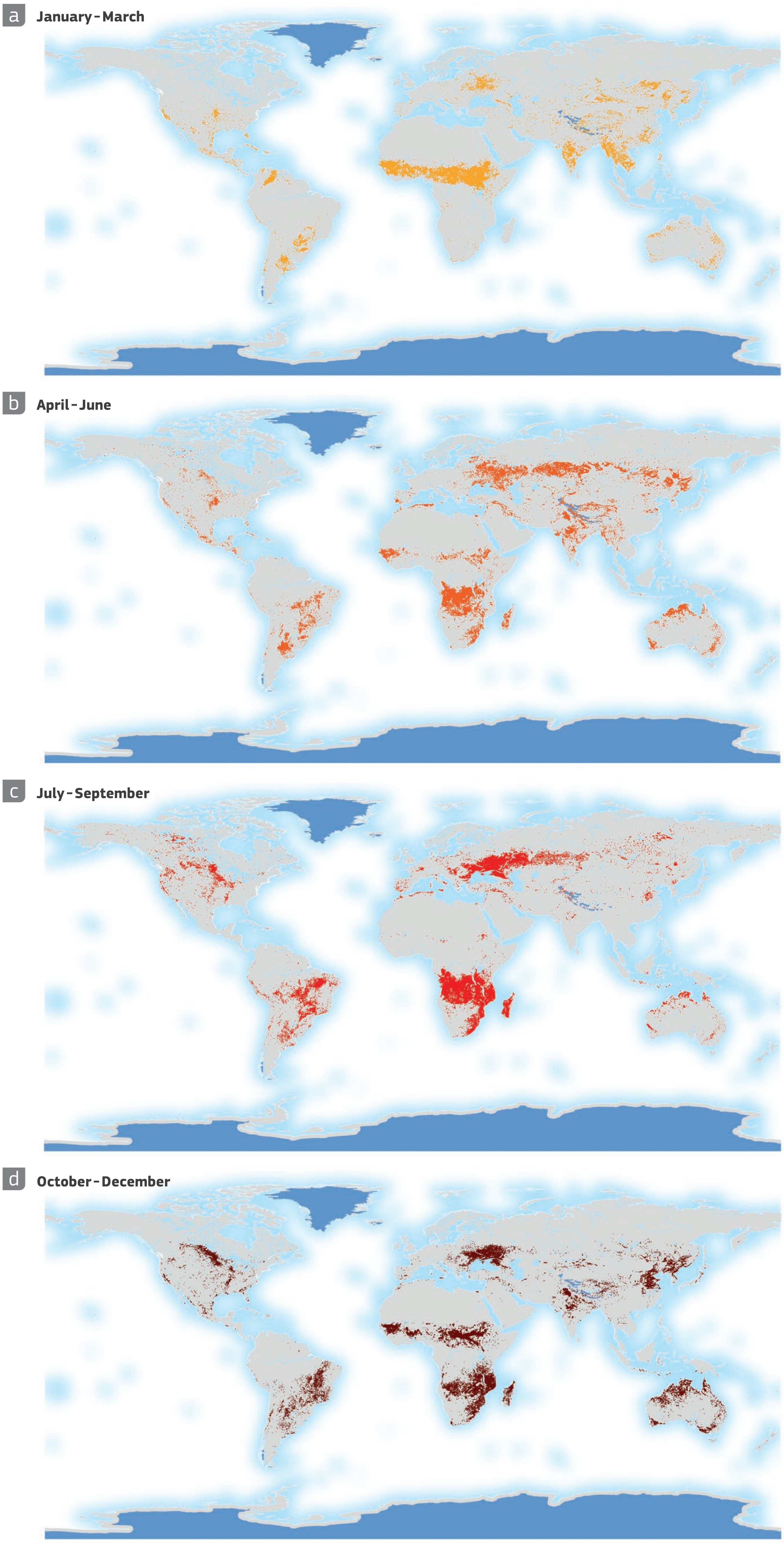
Post-fire land management near Sever do Vouga, Portugal. The picture shows commercial terracing operations. Tree stumps were removed while the slope was bulldozed into terraces (MMR).

Real-time fire monitoring

- Thanks to satellites, it is possible to monitor fire locations in real-time worldwide, and get a clear overview of which parts of the globe are burning. One of the most reliable systems is the Fire Information for Resource Management System (FIRMS). [154]
- FIRMS was developed by the University of Maryland, with funds from NASA's Applied Sciences Program and the United Nations Food and Agriculture Organization (FAO), to provide near real-time active fire locations to natural resource managers that faced challenges, by obtaining timely satellite-derived fire information.
- Global maps showing fire activities are available within three hours of a satellite overpass. On the map, each active fire location represents the centre of a 1-km pixel that is flagged as containing one or more fires.



A satellite image captures smoke and heat from wildfires in Colorado and New Mexico (USA). (NASA)



(**a–d**) Quarterly evolution of burnt areas in 2014. The maps of burnt areas are derived from the MODIS (Moderate-Resolution Imaging Spectroradiometre) Burned Area product distributed by the University of Maryland (USA). (IL, JRC, LJ) [155]

Soil erosion

Numbers of soil erosion

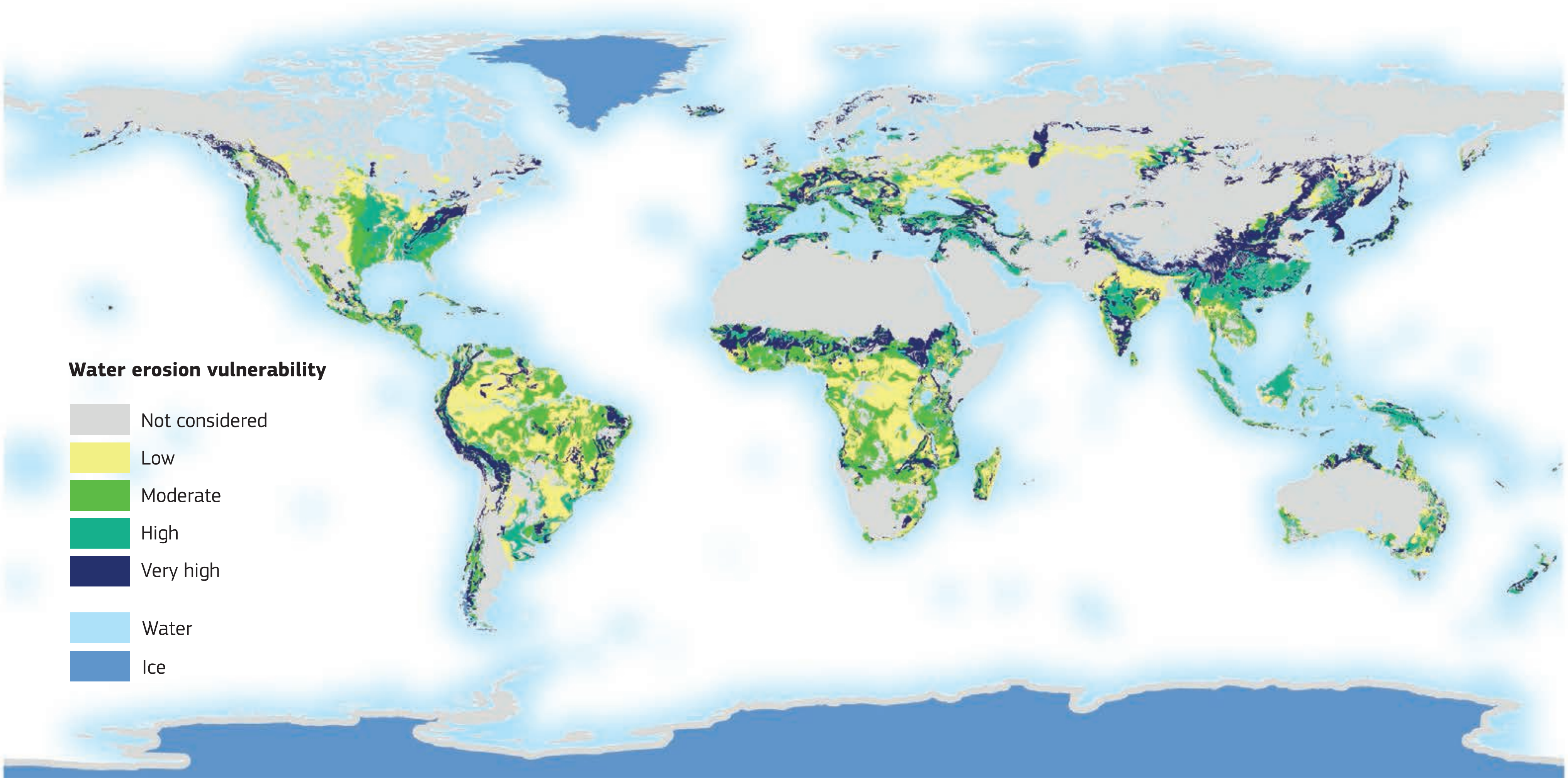
Soil erosion caused by wind and water is a widespread problem impacting ecosystems worldwide, including cultivated land, forested areas and rangelands. Recent estimates suggest that 80 % of the Earth's agricultural lands (see page 88) suffer from moderate to severe erosion, with more than 75 thousand million tonnes of fertile soil lost per year, a rate that is 10-20 times higher than the estimated rate of natural soil formation. Globally, soil erosion is the leading cause of agricultural lands becoming degraded and, ultimately, abandoned; each year, 10 million hectares of croplands have to be abandoned once the soils become so eroded that they can no longer support sufficient agricultural production. [156]

Although soil erosion is a naturally occurring process, it can be greatly accelerated by human activities, including tillage, removal of vegetation cover, soil compaction and overgrazing by livestock (see pages 122-125), particularly when these practices are conducted on steep slopes in areas subjected to intense rainstorms or wind events. Due to management practices, and climate and soil conditions (see Chapter I), rates of soil erosion can be particularly high in croplands of Asia, Africa and Latin America, which on average suffer 30-40 tonnes per hectare of soil loss per year. Soil erosion not only leads to land degradation, it can also reduce water quality and contribute to human health problems associated with elevated inputs of dust into the atmosphere.

Impacts of soil erosion

The effects of soil erosion on the abiotic conditions of the soil environment are well known. Erosion by either wind or water reduces the soil depth (or at least plant rooting depths - see page 43) and the removal of surface horizons leads to declines in the concentrations of available nutrient and soil organic matter pools. Water infiltration rates and water storage capacities are typically reduced in eroded soils, leading to decreases in the overall soil water availability. The interacting effects of soil erosion also degrade soil structure and reduce porosity. This generates a positive feedback loop that contributes to further reductions in soil water availability. Together, these effects of wind or water erosion typically lead to marked declines in plant productivity, with corresponding direct and indirect impacts on soil biodiversity.

(**a**) Soil losses may be due to (**b**) wind erosion and (**c**) water erosion. Both these types of processes lead to negative effects on soil-living communities. (DEH, JDY, NRCSSD)



Water erosion vulnerability map. Most water erosion prediction equations are based on the amount and intensity of rainfall and on four additional factors. These factors are the ability of the soil to hold together, the surface cover (which provides protection from the forces of erosion), the distance for action (slope length) and the slope gradient. Almost all management solutions to erosion address one or more of these factors. Soil survey reports provide information about water erosion, including erosivity (K factor), soil loss tolerance (T factor) and slope gradient (derived from the USDA Natural Resources Conservation Service). (LJ, JRC) [133]

Effects of erosion on soil biodiversity

Soil erosion can alter the amounts and types of organisms living in soil through a variety of mechanisms. Perhaps most importantly, soil erosion preferentially removes organic-matter-rich topsoils (see page 10), eliminating or reducing a resource-rich habitat that supports many soil organisms. This impact on soil organisms will be particularly evident in soils that have thin organic horizons with underlying soil horizons that are inhospitable to soil biota. For example, high rates of water erosion can cause many tropical soils to lose their organic horizons, leaving behind the underlying horizons that are often too acidic, nutrient-poor and depleted in organic carbon stocks to support high levels of microbial or fauna biomass. Similarly, eroded soils that have reduced water availability and lower organic matter concentrations will typically have lower rates of microbial mineralisation of nitrogen and phosphorus pools (see page 105), further reducing plant-available nutrient concentrations. Similar positive feedbacks occur when erosion-induced reductions in faunal biomass, particularly decreases in the numbers of burrowing earthworms, further reduce water infiltration rates, thereby accelerating water erosion and associated soil degradation.

Convicted of soil erosion

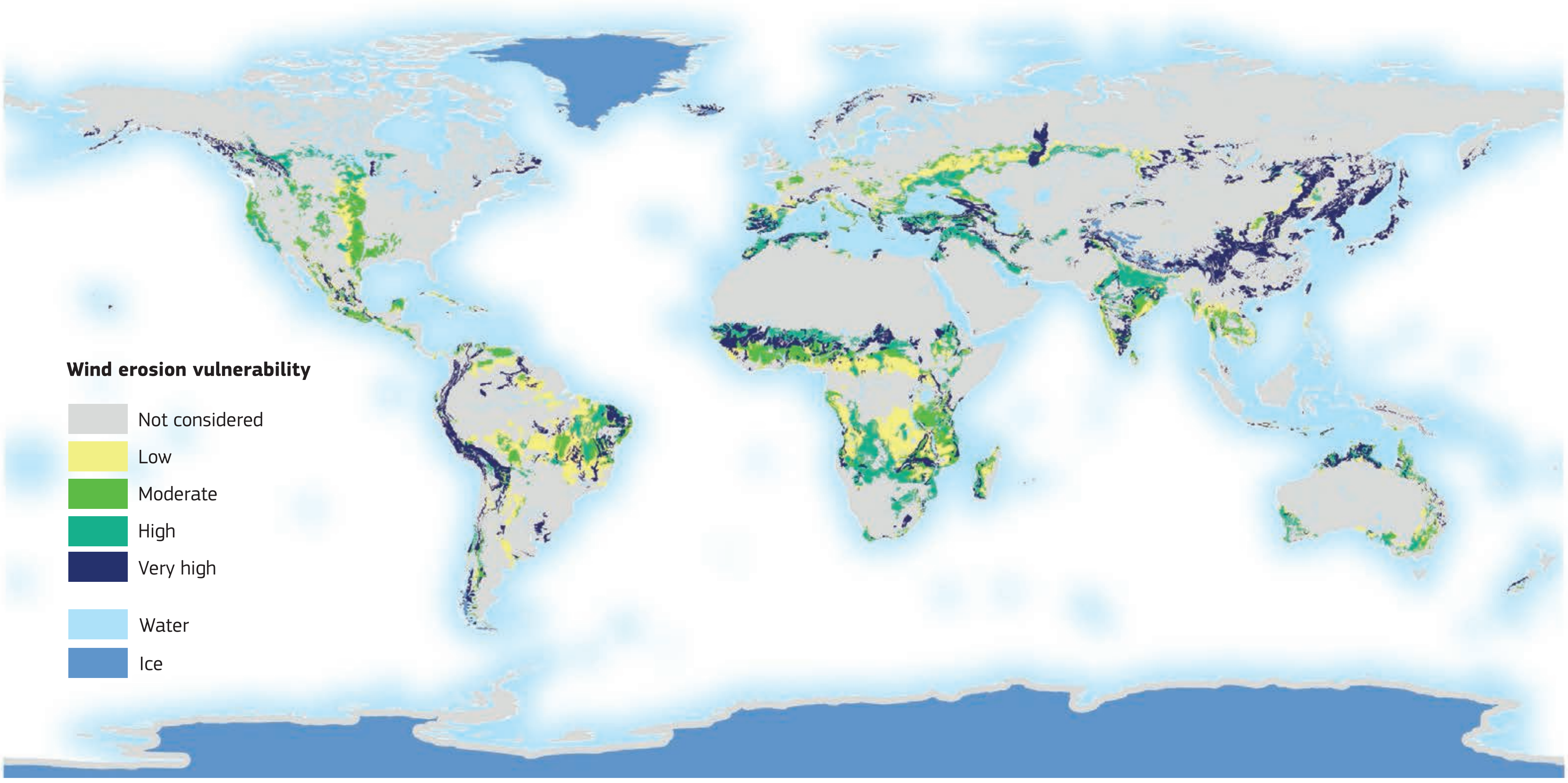
- Some soil organisms, such as some earthworm species, may also facilitate soil erosion by water.
- Charles Darwin was the first to observe that earthworms, under natural conditions, are able to cause erosion through the disintegration of the soil surface that then becomes more prone to runoff. In particular, the casting activities of some earthworms contribute to soil erosion.
- The species that produce labile casts favour surface sealing. These species are known as decompacting species as they produce granular casts.
- Decompacting species may also belong to other groups of soil organisms, such as enchytraeids, millipedes, ants and termites (see Chapter II).
- However, there is also a positive effect due to the tunnels burrowed by these species that increase soil porosity and water infiltration, thus delaying soil erosion.

Biological soil crusts, typical of drylands, are mainly formed by cyanobacteria and lichens. Because of the lack of vegetation cover, biocrust is particularly exposed to wind erosion. (DEL)

Wind can cause high rates of soil erosion in many arid and semi-arid ecosystems where soil surfaces are often unprotected from vegetation cover. The effects of this erosion on the diversity and function of belowground biota have been particularly well-documented. Biological soil crusts (see page 73) are common in arid and semi-arid ecosystems worldwide where complex communities of cyanobacteria (see page 35), mosses and lichens (see page 42) often cover the unvegetated soil surface. Biological soil crusts are particularly sensitive to the effects of wind erosion, especially in sandy soils, given that they are concentrated in a thin layer on the soil surface and are, therefore, sensitive to removal by wind or burial by wind-deposited sediments. Furthermore, biological soil crusts typically grow and re-establish slowly following disturbance.

The loss of these crusts via wind erosion can lead to prolonged decreases in the ecosystem services they provide, including: reducing water infiltration rates, decreasing seed germination, nitrogen fixation and carbon fixation (see Chapter IV).

Most strikingly, when biological soil crusts are damaged or fragmented by vehicles or trampling by humans or livestock (see pages 124-125), wind erosion rates often accelerate due to the loss of polysaccharides produced by cyanobacteria and fungi (see pages 38-41) present in these crusts that bind soil particles together. This generates a positive feedback whereby loss of biological soil crusts accelerates wind erosion, leading to further degradation of the biological soil crusts and the soils in these ecosystem types.



Wind erosion vulnerability map. When bare soils are subject to wind erosion. The shear force of wind detaches particles protruding from the soil surface, and these detached particles then strike other particles on the surface as they bounce along the surface. This process is called saltation and is the most noted transport mechanism for sand-sized particles. Soil survey reports rate the susceptibility of bare soil surfaces to wind erosion by assigning the soils to wind erodibility groups. These groups are shown in the tables of soil survey publications covering areas subjected to wind erosion. The groups are based on soil texture, organic matter content, effervescence of carbonates, rock fragments and mineralogy. Also considered are soil moisture, surface cover, soil surface roughness, wind velocity and direction, and the length of unsheltered distance that reflects the distance from the nearest obstruction to wind flow (derived from USDA Natural Resources Conservation Service). (LJ, JRC) [133]

Land degradation and desertification

A matter of climate and human activity

Desertification, according to the United Nations Convention to Combat Desertification (UNCCD), is defined as 'land degradation in arid, semi-arid, and dry sub-humid areas, resulting from various factors, including climate variations and human activity'. Therefore, desertification is a natural phenomenon exacerbated by human activities. Approximately 40 % of the world's land surface is covered by drylands (i.e. arid, semi-arid and dry sub-humid lands), which are home to approximately two thousand million people. Unfortunately, a large part of these lands are degraded, meaning that they are gradually losing their ecosystem functioning and productivity. This can eventually lead to desertification, which is the most severe form of land degradation. With increasing pressure on the landscape due to a growing population and economic development, this can have devastating impacts on rural livelihoods. [157]

UN Convention to Combat Desertification

- The United Nations Convention to Combat Desertification (UNCCD) is a global treaty to combat desertification and mitigate the effects of drought through national action programmes.
- The UNCCD was adopted in Paris, France on 17 June 1994, and entered into force in December 1996.
- The UNCCD has 195 parties, making it a truly global convention. All member states of the UN are parties to the convention. Canada was the only country in the world to leave the agreement in 2013.
- To help publicise the convention, 2006 was declared 'International Year of Deserts and Desertification'.
- The UNCCD facilitates cooperation between developed and developing countries, particularly regarding knowledge and technology transfer for sustainable land management, in order to reduce land degradation.

Drivers of land degradation

There are many drivers of land degradation, including overgrazing by animals (see pages 124-125), which leaves the soil bare as well as compacted through trampling of livestock's hooves, thus making it difficult for water to infiltrate into the ground. Further unsustainable human activities, including agricultural use of steep slopes and excessive irrigation, can lead to salinisation of the soil and erosion (see pages 128-129). Climate change (see pages 132-133), drought, and flooding further accelerate land degradation in these fragile systems. The more exposed the soil as the vegetation cover disappears, the more the degradation perpetuates; for example, through wind erosion when the ground is left unprotected or through water erosion when it rains and the water is not able to infiltrate into the soil, creating gullies and rills, especially on slopes.

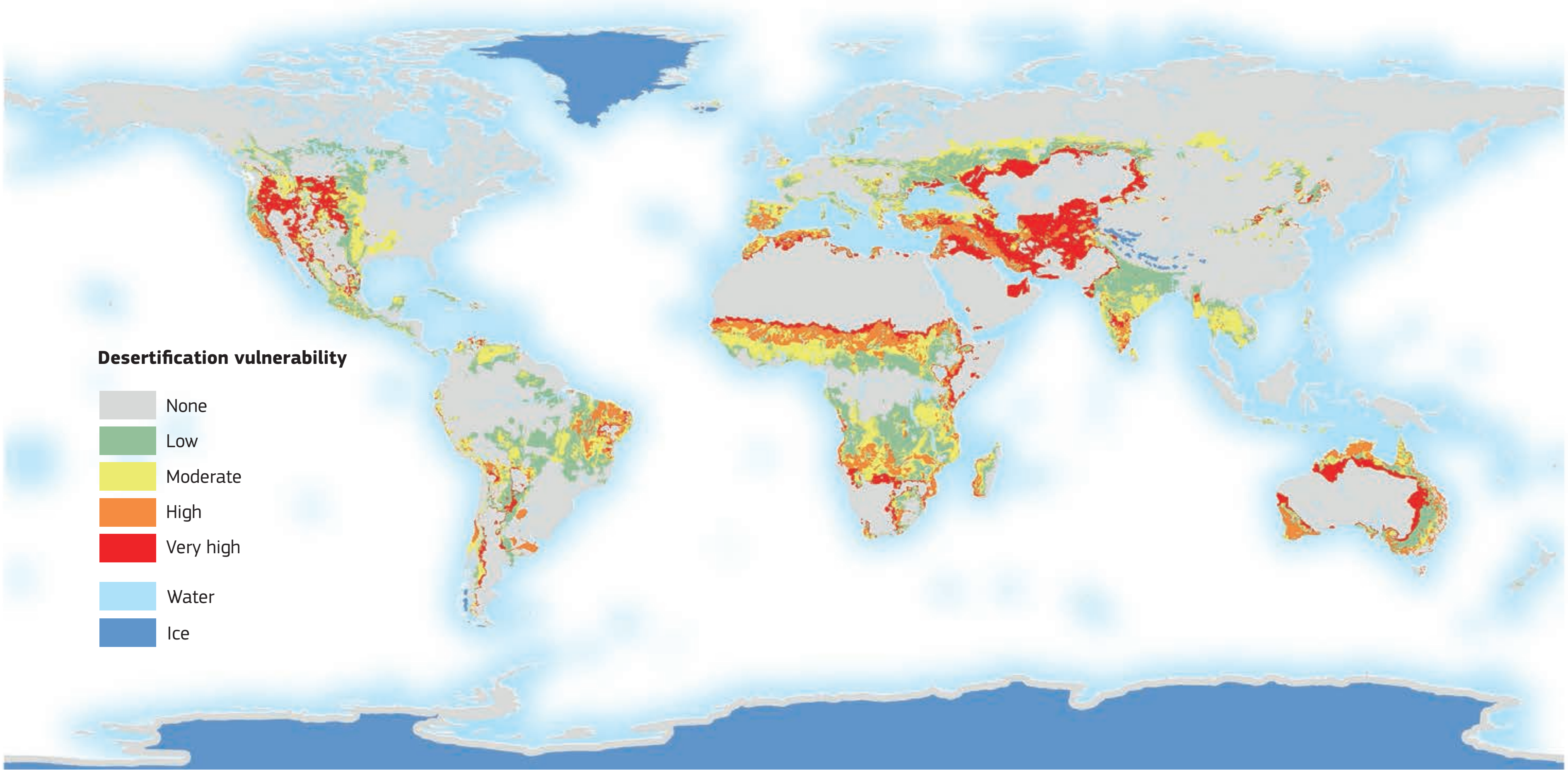
Desertification is defined as 'land degradation in arid, semi-arid, and dry sub-humid areas, resulting from various factors, including climate variations and human activity'. (UNIDO)

Through this type of erosion, the nutritionally rich top layers of the soil are lost, the very layers that support soil biota. Increasing fire occurrence (see pages 126-127) changes the cycling of nutrients and biological and physical soil characteristics, including loss of structure and soil organic matter (SOM – see pages 102-106). These changes can also have indirect impacts, such as increased water repellency of the soil, decreased infiltration and increased runoff, which in turn lead to erosion and further desertification. Most feedbacks between dryland plant communities and soil fertility are linked to their mutual interaction.

Two different groups of feedback have been identified. Firstly, a high allocation of carbon and nutrients to a deep, strong and dense root system together with a notable plant cover and investment in soil microbes and enzyme production has a positive effect on soil fertility. Secondly, albeit by contrast, high retention of nutrients in standing biomass and high C:N ratios (see page 106) in litter prevent the rapid release of nutrients from the SOM, thus slowing soil microbial processes and lowering fertility.

Increased drought reduces the first group of positive properties for soil fertility and protection, but intensifies the second group of negative properties. In the short-term, drought can increase SOM by increasing the total amount of litter and dead roots. Long-term experiments suggest that SOM decreases through the reduction of plant cover, implying a decrease in litter and an increase in soil erosion. Microbial activity is sensitive to drought. As the thickness of the water film around soil particles is reduced, diffusion and access to nutrients become more limited. Decreases in soil enzyme activity and respiration have been widely observed.

Drought occurs when a region's water supply is insufficient for an extended period of time. Intense drought can cause significant damage to ecosystems and promote degradation and desertification processes. (AQU)



Desertification vulnerability map. The vulnerability was assessed through biophysical properties (i.e. soil type and climate – derived from USDA Natural Resources Conservation Service). (LJ, JRC) [133]

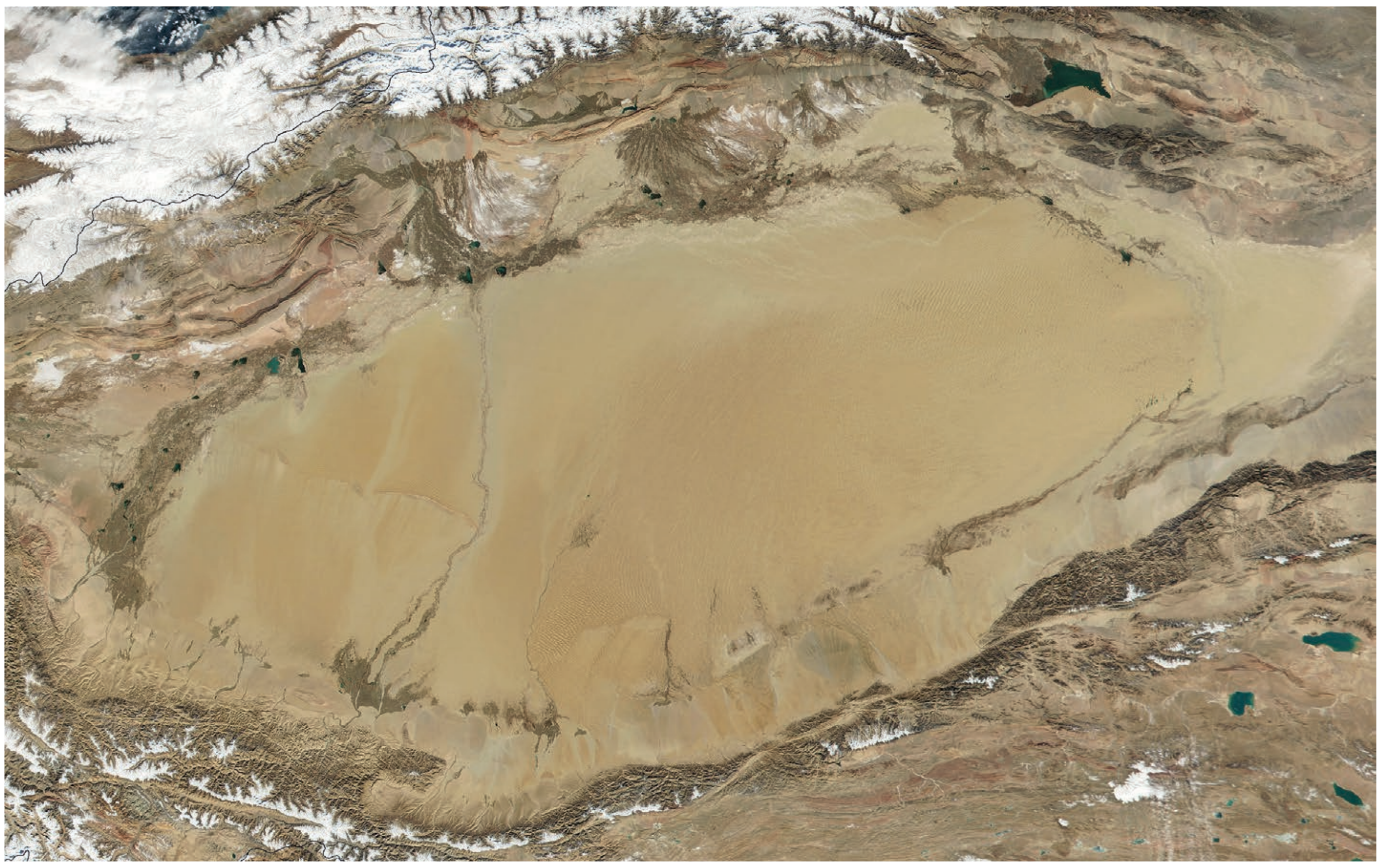
Effects on soil biodiversity

Soil bacteria and fungi (see pages 33-35, 38-41) have developed strategies to survive desiccation and rewetting, including:

a. accumulation of osmoregulatory substances that block water losses
b. slime production that slows down desiccation processes
c. production of dormant life forms, such as spores (see box on page 34)

Drought tolerance may also result from morphological life forms. With hyphal networks (see box on page 39) that can cross air-filled soil pores to access nutrients and water from different locations, fungi are generally considered to be more resistant to desiccation than bacteria. Some studies reported that fungi became more abundant than bacteria when soils were drier. Both are capable of rapid activation upon rewetting, and play a role in the mineralisation burst that causes the soil carbon dioxide (CO_2) efflux pulse following rewetting.

In Californian grasslands, the present and potentially active soil bacterial and fungal communities were tracked over a season. The potentially active bacterial community changed significantly as summer drying progressed, then returned to pre-drying composition within several hours of rewetting, displaying spectacular resilience (see page 97). By contrast, the fungal community was not detectably different among sites and was largely unaffected by dry-down, showing marked resistance to desiccation.



Satellite images of the Taklimakan Desert in northwest China. This is a vast region of sand desert sitting in a depression between two high mountain ranges (the snow-covered Tien Shan Mountain in the north and the Kunlun Mountains in the south). Desertification and shifting sand dunes are a major concern for the farmers and grazers who live at the desert's edge. (BIG/NASA)

Hyphal network of mycorrhizal fungus covering plant roots. These fungi are sensitive to land degradation, and their reduction in drylands can affect the whole food web as they influence the growth of plants, which produce the main inputs to the food web. (APP)

Of particular interest is the behaviour of a specific group of soil fungi, the mycorrhizal fungi (see page 40), in degraded areas. Mycorrhiza are symbiotic associations between the roots of most plant species and fungi. In dry and nutrient-poor ecosystems, mycorrhiza are critical for the improvement of drought resistance and prevention of desertification. However, mycorrhizal fungal communities are also sensitive to soil degradation and summer drought. Both reduce mycorrhizal density but usually the communities do not disappear, thus suggesting a certain degree of adaptation to stress. Mycorrhizal fungi may be the keystone microbe in dryland ecosystems. In fact, if plant carbon inputs are the major control of the soil food web (see page 96), then mycorrhiza could indirectly alter bacterial and fungal abundance and functionality by influencing plant growth. This shows the risks associated with the loss of such a group of soil organisms because of the land degradation and desertification.

By reducing primary production (e.g. plant growth), drought limits food resources in the soil food web, influencing soil animals and the services to which they contribute. Soil fauna (see Chapter II) are also directly influenced as they are adapted to a high-humidity interstitial environment. Earthworms and enchytraeids (see pages 48, 58) are not active in dry soil. Protists and nematodes (see pages 36-37, 46-47) are only active in the water films surrounding soil particles. Short-lived and smaller species were found to be better adapted to drought, as they can access smaller pores where water is held and can recover quickly after drought. Microarthropods (mites and collembolans) inhabit the air-filled spaces between soil particles but their life histories are still affected by drought, with shorter-lived opportunistic microarthropods dominating drought-affected areas.

In conclusion, changes in soil moisture availability may alter trophic patterns within soil communities. Drought ultimately reduces root-mediated energy pathways through herbivores and predators. Some studies indicated changes in ratios between fungal and bacterial channels of the food web. This can have important implications on how tightly nutrients, such as nitrogen, are cycled, as bacterial-mediated decomposition pathways are 'leakier' than fungal-mediated pathways. Decreases in the role of fungal pathways in decomposition and nutrient-cycling dynamics may also influence soil structure and the storage of organic C and N within soils.

The structure of soil fauna communities, such as collembolans, is affected by the reduction in food resources in degraded and dry soils. (AM)

a

b

Impoverishment of soils due to (**a**) depletion of soil organic matter (resulting in soils with pale brown colour) is a leading cause of long-term soil degradation in drylands. In this condition (**b**) the scarce vegetation cover, one of the first signs of ongoing desertification, is incapable of restoring the soil organic matter pool. (RHA/NPS, MBD)

Climate change

A few numbers on climate change

Climate change refers to a statistically significant variation in either the mean state of the climate or in its variability, persisting for an extended period of time (typically decades or longer). Climate change may be caused by natural processes or persistent anthropogenic processes that cause changes in the composition of the atmosphere. The most evident effect of climate change is a variation in temperature. Warming of the climate system since the 1950s is unequivocal, many of the observed changes are unprecedented over decades or millennia. Furthermore, the number and strength of recorded extreme events (e.g. heat waves, droughts, tornadoes and hurricanes) have increased. Each of the past three decades has been successively warmer at the Earth's surface than any preceding decade since 1850. The period from 1983 to 2012 was most likely the warmest 30-year period of the past 1 400 years in the Northern Hemisphere, where such assessment is possible. The globally averaged combined land and ocean surface temperature data show a warming of 0.85 °C over the period 1880 to 2012. All of the above, of course, also has an impact on terrestrial ecosystems, including soil. [158-161]

Effects on soil biodiversity

Climate change is one of the most important factors of environmental change that will influence soil biodiversity and ecosystem functioning in the coming decades. However, predictions of the consequences of climate change for soil biodiversity are highly complicated by the many features that may covary with climate change. For example, climate change is preceded by a gradual increase in global carbon dioxide (CO_2) levels, which have an influence on plant species composition, as well as on the resource quality of the dead organic matter that is entering the soil.

Climate change may also operate in a large variety of ways, from changed onset of spring warming to a delayed onset of winter, and from a reduced number of frost days to an increased number of extreme (drought or rainfall) events. Moreover, climate change effects may have different responses depending on the type of biome. For example, warming effects on arid or Mediterranean ecosystems (see page 83) may reduce soil biodiversity, whereas the warming of Arctic tundra (see page 85) could enhance soil biodiversity. Therefore, it cannot be generalised that climate change always causes soil biodiversity to decrease or increase. The current scientific literature includes a number of examples of studies addressing numerous aspects of climate change.

However, the studies are still not exhaustive; therefore, a complete overview of all possible consequences of climate change cannot yet be provided. Nonetheless, there are a number of case studies available that may be used to work out several possibilities of climate change effects on soil biodiversity. Here we provide a number of such cases in order to obtain a first overview of the possible effects of climate change on soil biodiversity. In the near future, when more studies have been carried out, we may obtain a more complete understanding of climate warming effects on soil biodiversity, wherever possible classified by ecosystem type and geographical position.

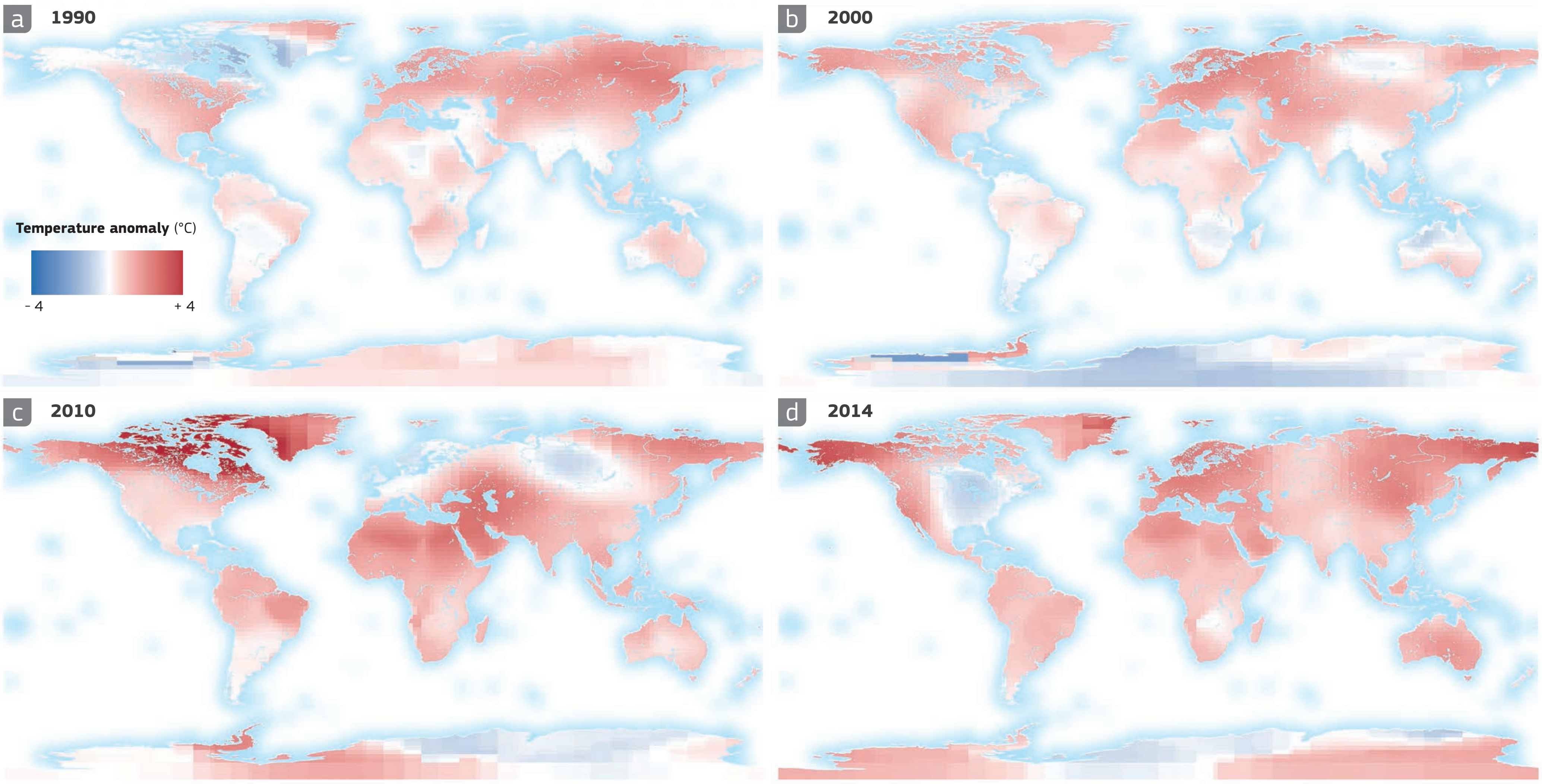
In a two-year warming study analysing grassland communities, it was shown that a 3.5 °C temperature increase had little effect on soil respiration and plant biomass aboveground, but the increased root growth had clear effects on the soil fauna. For example, earthworms (see page 58) and some groups of mites (see page 49) decreased in numbers, whereas enchytraeids (see page 48) migrated to deeper soil layers. Soil fauna responses to warming would not be generalised, as individual groups differed in their responses. However, epigeic earthworm species completely disappeared from the plots exposed to warming, whereas the diversity of fungivorous mites increased. All together, the composition and trophic structure of the faunal community changed substantially as a consequence of warming, and the systems became more fungal-dominated.

Increasing temperatures tend to lead to fungal-dominated systems, thus promoting fungivorous species. However, the fact that some fungivorous mites (e.g. Prostigmata) are severely reduced under warmer conditions suggests that, for certain species, they have no effective strategy to adapt to changes in soil temperature and moisture. (GSM)

In a grassland steppe in Inner Mongolia, China, the effects of climate warming by infrared radiators and shifting precipitation on the abundance, richness and composition of the entire bacterial kingdom (see pages 33-35) were examined. The study took five years. Watering had a greater effect than warming. Acidobacteria and Gammaproteobacteria were most sensitive to the environmental changes. The authors tried to dissect both direct and indirect effects of climate change. The analyses further revealed that increasing soil water content altered the richness of bacterial groups directly, whereas community composition of bacterial communities was indirectly influenced by reduced soil nitrogen content and increasing soil pH.

In Tennessee (USA), special chambers are constructed in order to manipulate CO_2 and temperature and register the effects on soil organisms and plants. (PK)

In established fields in Tennessee, USA, the effects of CO_2 increase, warming and altered precipitation on vegetation, soil communities and soil processes were studied. The effects of single factors, as well as their combined effects, were studied in this outdoor experiment. Water had the strongest effect dominating both CO_2 enhancement and warming effects. The strongest effects on soil communities and soil processes were seen in changes in both the plant community composition and functioning of individual plant species. Both soil enzyme activities and nematode (see pages 46-47) community composition were studied. Drought influenced enzyme activities and nematode numbers in specific ways, with generally stronger effects than those of temperature. Interestingly, the effects of individual plant species on enzymes and nematode numbers were so variable that some plant species could re-set the effects of drought or warming. Therefore, the authors conclude that assessment of the effects of climate warming on soils requires an understanding of the effects of warming on plant distribution, plant functioning and plant community composition, as these may reinforce, or counteract, the effects of climate change on soil biodiversity.



Maps of temperature anomalies in recent years. These maps depict how much warmer or colder a land region was in (a-d) 1990, 2000, 2010 and 2014 compared to the norm in the same region from 1951-1980. These maps do not depict absolute temperature but instead show temperature anomalies, or how much temperatures have changed (derived from NASA Earth Observations). (LJ, JRC) [162]

Climate change and migration

Climate warming influences current range shifts (i.e. migration to areas with more suitable climatic conditions) of many plants and animals. However, little is known about climate-warming effects on soil biodiversity through dispersal-mediated range expansion of soil biota.

In a study of the European coastline, root-feeding nematode communities of the dune grass *Ammophila arenaria* were found to be the most diverse in north-western Europe. In the Netherlands and Wales, there were eight species of root-feeding nematodes, including all major feeding types varying from ecto- to semi-endoparasites, migratory endoparasites, as well as root knot and cyst nematodes (see pages 46-47). Interestingly, towards the Mediterranean the number of root-feeding nematode species declined and inclued either root knot or cyst nematodes, but both sedentary endoparasites were not present at the same time in the south. Along the European coast, where nematodes and plant materials will be dispersed by sea currents, dispersal of plant genotypes and nematode species may be less constrained than anywhere on the mainland.

(**a**) Nematode (indicated by the yellow arrow), stained by means of acid fuchsin, feeding on roots of (**b**) *Ammophila arenaria*, have been studied to investigate the possible range shifts in Europe. Range shifts occur when animal move in response to climate change. (SRE, GLA)

Nevertheless, many plant species are increasingly dispersed from lower to higher latitudes and altitudes. It has been demonstrated that, in the new range, some well-established range-shifting plant species have left behind their natural soil-borne enemies. In a phylogenetically controlled study, the rhizosphere community of range-expanding plant species was compared with that of plant species belonging to the same genus and native to the invaded range. It was shown that range-expanding plants had less fungal hyphal biomass (see box on page 39) and lower amounts of *Fusarium* spp. in the rhizosphere than similar plants. Also, bacterial community composition in the rhizosphere of range expanders differed from that of native plants. However, it remains unknown how well soil communities may disperse with climate warming and how they may become established in the new range.

Future trends

- On the basis of several scenarios exploring alternative development pathways and covering a wide range of demographic, economic and technological driving forces, future greenhouse gas emission trends and mean temperatures can be estimated.
- A range of scenarios concur that it is more than likely that the mean global surface temperature for the period 2081–2100 will be more than 1.5 °C above the mean for 1850-1900. [163]
- Such climate modifications could strongly impact soil organisms either directly, through effects on their ecology, or indirectly, through increased floods, droughts, wildfires, land-use changes and fragmentation of natural systems. An increase in soil erosion rate is also expected.
- Climate change is likely to have significant impacts on soils that may affect all of the services provided by soil biodiversity (see Chapter IV). Unfortunately, a precise quantification of these impacts is not possible at the moment. In any case, all mitigation and attenuation measures taken to limit global climate change are expected to have a beneficial impact on soil biodiversity conservation, soil functioning and associated services.

Climate change and extreme environments

Climate change can make extreme environments more accessible, which may enable species with novel traits to enter with possible cascading effects on soil biodiversity and ecosystem functioning.

For example, biomes in cold climate regions currently become increasingly colonised by nitrogen-fixing plant species, such as the genera *Lupinus* and *Alnus*. The nitrogen-binding activity of the root symbionts (see box on page 99), strongly changes nitrogen (N) availability. The effects on soil biodiversity have not yet been systematically studied, but it is expected that the decomposition process (see page 106) will change from fungal-based to bacterial-based, which has substantial consequences for further ecosystem changes in these boreal ecosystems (see page 79). Such plant invasions (see page 119) may alter the regional C and N cycles substantially (see pages 104-105), increasing water consumption and air pollution, with subsequent impacts on biodiversity.

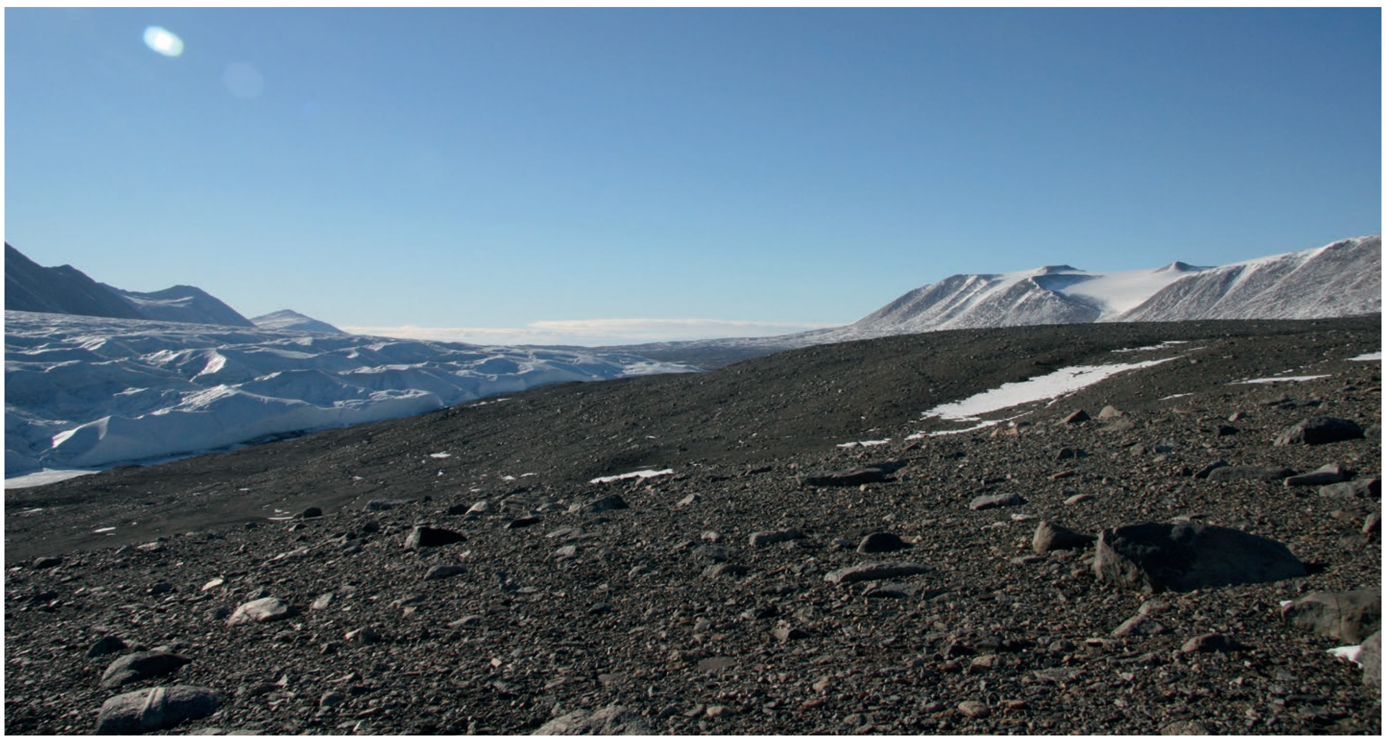
Many studies on the effects of climate change on soil biodiversity have been carried out in Antarctica (see page 86), where climate change has had astonishing effects on soil communities. Although most of Antarctica is warming, some areas are cooling, and there are pulses of wet years. This cooling has had a strong impact on the most abundant nematode (see page 70) species, *Scottnema lindsayae,* which has seen population shifts over the past twenty years with important consequences for soil carbon dynamics. However, with pulses of warming, there is some uncertainty as to whether the populations will rebound. In Antarctica, soil biodiversity can be studied in the absence of vegetation changes. In the Antarctic polar desert of the McMurdo Dry Valleys, Taylor Valley is dominated by large expanses of dry, saline soils. During the austral summer, melting glaciers, snow patches and subsurface ice supplies water to ephemeral streams and wetlands. In one year, an ephemeral stream, Wormherder Creek, produced an exceptionally high-flow event that altered soil properties and communities. The flow of water increased soil water availability and decreased salinity within the wetted zone compared to the surrounding dry soils. The leaching of salts through flooding reduced stresses to levels that are more favourable for soil organisms, improving habitat suitability, which had a strong positive effect on soil-animal abundance and diversity. Moreover, the moisture gradient created greater connectivity within the landscape, which may promote soil fauna dispersal.

Climate change and food web

Soil food web interactions (see page 96) complicate the responses of soil biodiversity to climate change. Climate change may influence individual species, which can change the outcome of species interactions when competing for the same resource. However, when the species that benefits most from warming is preferentially grazed, the effects of warming might be re-set.

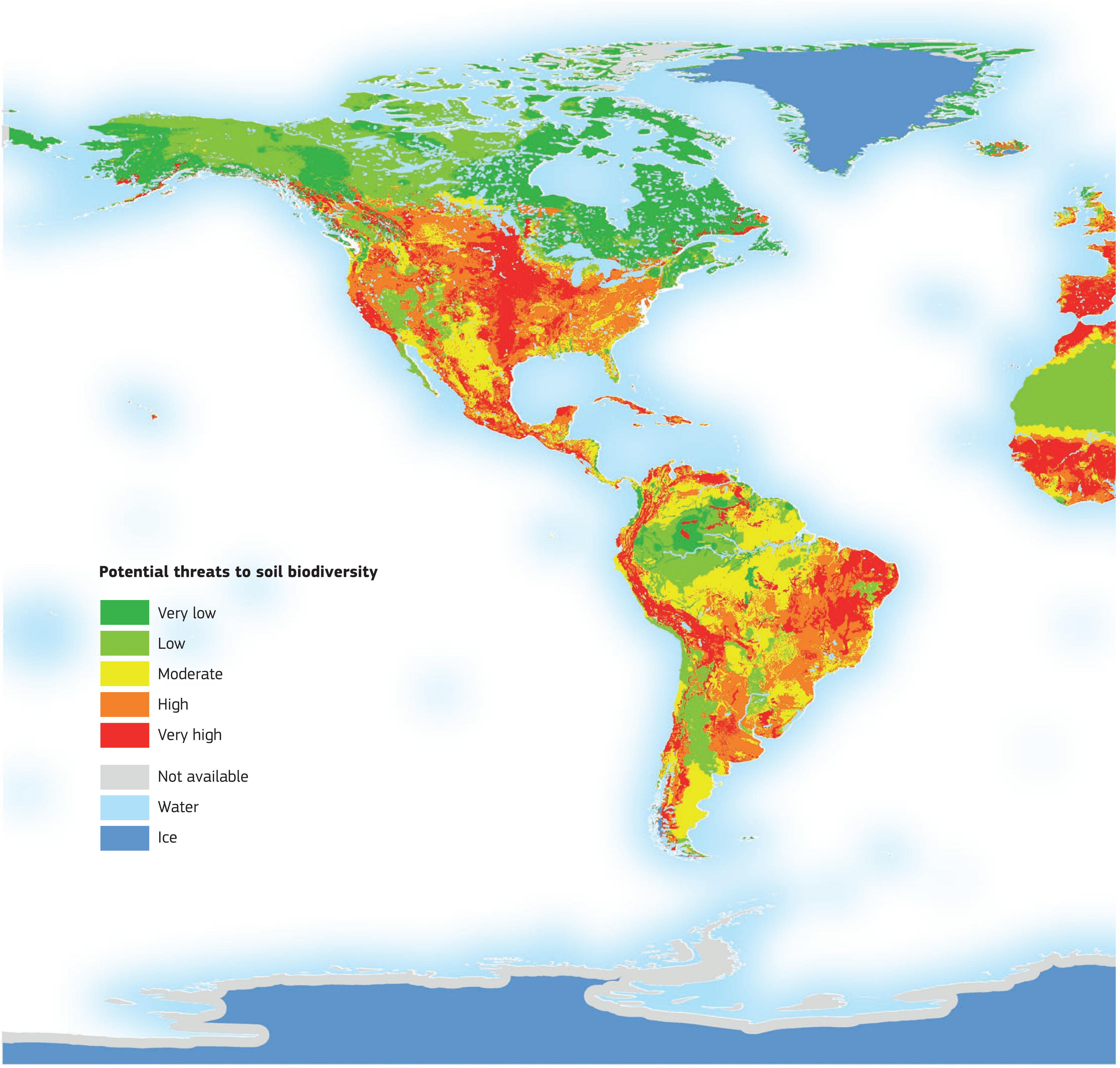
The fungal species *Hypholoma fasciculare* grows less in warmer temperatures. This can affect other components of the soil food web, such as collembolans, that feed on it. (JHM)

This is nicely illustrated by a recent study on saprotrophic fungal communities (see pages 38-41). The composition of fungal communities is a consequence of competitive fungal interactions, and is also a major determinant of woodland decomposition and nutrient-cycling rates. An elevation of atmospheric temperature is predicted to drive changes in fungal community development. Fungal growth, however, can also be regulated by fungal grazers, such as collembolans and isopods (see pages 50, 56). Warming has promoted the competitive ability of one fungal species, but this fungal species was preferentially grazed by all invertebrates. As a consequence, a multispecies assemblage of fungi was maintained by grazing, even though one fungal species was competitively superior under warming. Decomposition was, however, enhanced under warming. The conclusion is that the effects of climate warming on complex communities might be buffered by (unpredictable) alterations of species interactions. Therefore, further investigations are needed to better understand these relationship mosaics.



Taylor Valley in Antarctica has dry and saline soils with no vegetation. The effects of climate change on soil organisms are well studied in this region. (BKI)

Map of potential threats to soil biodiversity



Mapping potential threats to soil biodiversity

Although the role of soil organisms in providing key ecosystem services is increasingly recognised, several factors can affect the health and vitality of soil-living communities. While scientific knowledge on the effect of potential threats is advancing all the time, a geographical evaluation of the global distribution of these potential threats to soil biota is still lacking.

The lack of this type of assessment might be due to the complexity of soil biodiversity itself. As seen in Chapter II, soil communities are extremely diverse. Therefore, a risk to one specific group of soil organisms may be irrelevant to another. In addition, apart from the soil surface, the majority of the 'habitat' is underground and out of sight. Furthermore, many of the potential pressures are difficult to map as they result from the interactions of several factors (e.g. it is very difficult to map climate change).

Many environmental factors (e.g. temperature, land cover) are now relatively easy to map and monitor through the vast quantities of data collected by various satellite-based sensing systems. However, such tools are unable to provide direct information relating to the state of soil organisms. In addition to these conceptual problems, the issue of mapping risks to soil biota is further complicated by the lack of a clear and recognised list of the risks that can considered to be real threats to soil organisms and, consequently, the level to which each impacts soil life.

This atlas has collected information from a group of soil biodiversity experts on potential risks to soil life. The list of threats presented in Chapter V includes those that, at the moment, can be considered as the most relevant and represent a good approximation for a preliminary assessment of potential risks to soil biodiversity.

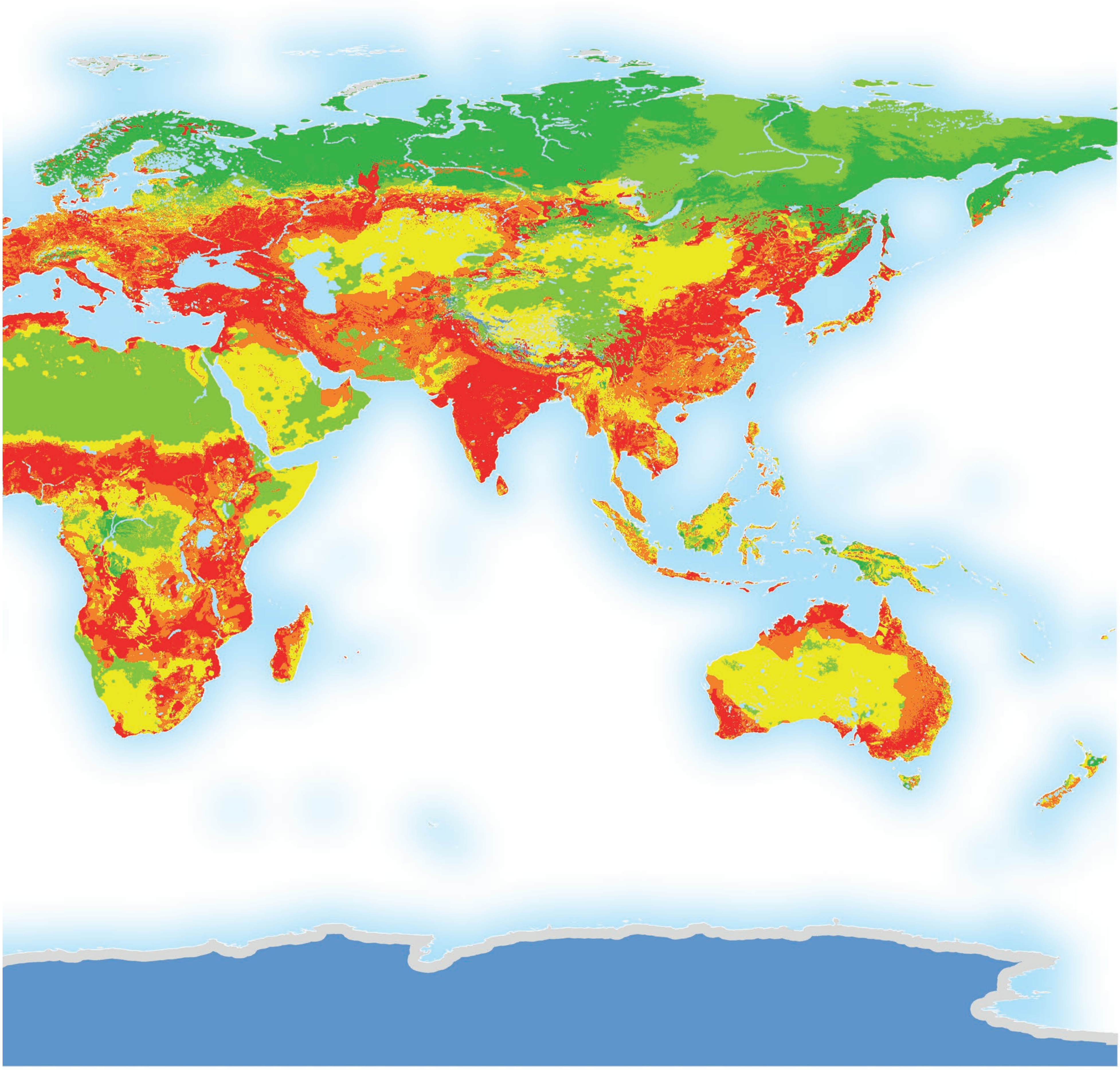
In this context, the map on this spread is a first attempt to map potential threats to soil biodiversity at a global scale. However, the practical use of this type of map depends on the simultaneous development of systems to monitor soil biodiversity distribution. We can only assess what is under threat if we first know what is there.

Methodology

As seen in Chapter V, there are numerous pressures that can potentially alter soil life. However, it is difficult to obtain a reliable distribution assessment for many of them because 1) there are several factors determining individual pressures and 2) global scale data are often lacking.

The intensive use of soil in agriculture, for example, depends not only on the distribution of croplands, but also on the adopted agricultural practices (e.g. tillage system, fertilisers and pesticide load), which are not always easy to map at the global scale. Therefore, simple proxies were needed in order to spatially represent each of the selected potential threats.

In this context, for example, indices such as the Global Aridity Index, expressed as a generalised function of mean annual precipitation and potential evapotranspiration, can be used as proxy to visualise the distribution of soils potentially affected by climate change.



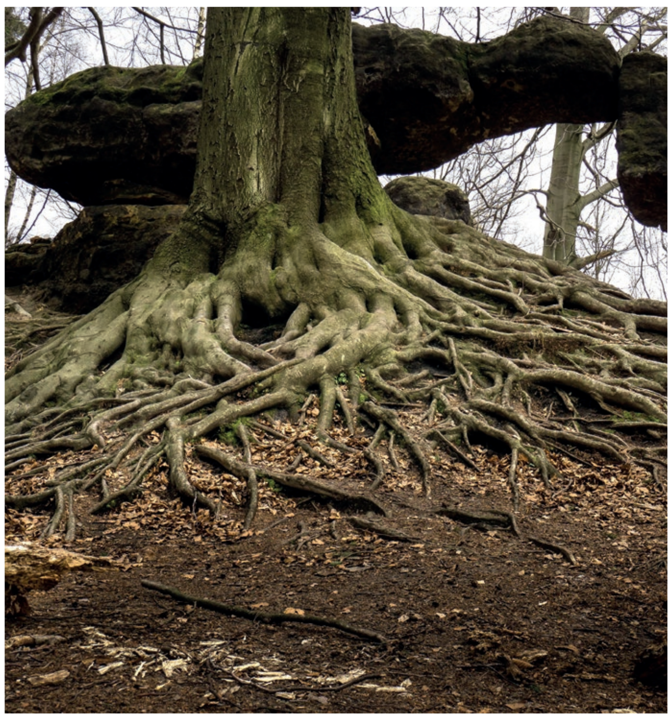
For the development of this map, the following threats and corresponding proxies were chosen:

- loss of aboveground biodiversity: map of plant species loss developed by the University of Maryland, Baltimore County (UMBC) [143]
- pollution and nutrient overloading: map of the nitrogen fertiliser application developed by the NASA Socioeconomic Data and Applications Center (SEDAC) [164]
- agricultural use: map of cropland percentage cover developed by the International Institute for Applied Systems Analysis - International Food Policy Research Institute (IIASA - IFPRI) [149]
- overgrazing: map of cattle density developed by the International Livestock Research Institute (ILRI), the Food and Agriculture Organization of the United Nations (FAO) and the Free University of Brussels (ULB - LUBIES) [152]
- fire risk: map of fire density 1997-2010 developed by the United Nations Environment Programme Division of Early Warning and Assessment (UNEP - DEWA) [165]
- soil erosion: map of Water and Wind Erosion Vulnerability Indices developed by the United States Department of Agriculture Natural Resources Conservation Service (USDA - NRCS) [133]
- land degradation: map of Desertification Vulnerability Index developed by the United States Department of Agriculture Natural Resources Conservation Service (USDA - NRCS) [133]
- climate change: map of Global Aridity Index developed by University of Leuven (UKL), with the support of the International Water Management Institute (IWMI) and the International Centre for Integrated Mountain Development (ICIMOD) [166]

All datasets were then harmonised on a 0 - 1 scale and summed, with total scores categorised as very low, low, moderate, high or very high level of threat to soil biodiversity.

Results

The result is an initial attempt to denote levels of potential risk to soil biodiversity at a global scale. The pattern reflects the discussion in this chapter on the main potential threats to soil life. The areas with the lowest level of risk are mainly concentrated in the northern part of the Northern Hemisphere. These regions are generally less subjected to both direct (e.g. agriculture) and indirect (e.g. climate change) anthropogenic effects. At the opposite end of the scale, the areas with highest risk are those with the greatest exposure to human activities. An important point to highlight is the nature of risk shown in the map. As indicated, the potential rather than the actual level of threat has been mapped. This means that in the areas with high or very high levels of risk, soil organisms may not necessarily be in real danger. However, these areas present a combination of factors that lead their soils, and thus the organisms living in them, to be more sensitive to risk. In conclusion, this map will require much more effort to improve both its reliability and resolution. Furthermore, in order to be useful for conservation purposes it will need to be accompanied by a reliable assessment of the global distribution of soil biodiversity. However, despite these limitations, the map represents a preliminary global assessment of the risk to soil life.



Different management practices may help preserve soil biodiversity, from low-input agriculture, crop diversification, use of organic amendments, afforestation, soil erosion control and conservation of aboveground biodiversity hotspots. The application of such practices can allow soil organisms to contribute to the provision of ecosystem services. (CKE/NRCSSD, MSA, KWA, USFS, PZI, UKGP)

Introduction

A significant and increasing proportion of the Earth's land area is covered by crop- and rangelands. Agricultural landscapes hold a large proportion of the world's biodiversity, but knowledge of the relative contribution of each land management type to the conservation of soil biodiversity, the maintenance of ecosystem functions, and the provision of ecosystem services is limited. [167]

Soil is the critical and dynamic regulatory centre of the majority of ecosystem processes. Soil organisms contribute to a wide range of ecosystem services that are essential to the sustainable functioning of natural and managed ecosystems. As mentioned in earlier sections of this atlas, highly diverse soil biological communities are largely linked to the high diversity of niches found in the soil environment, which are fostered by the extremely high physical and chemical heterogeneity at small scales, as well as the different microclimatic characteristics and functions of organisms that promote the development and maintenance of niche diversity.

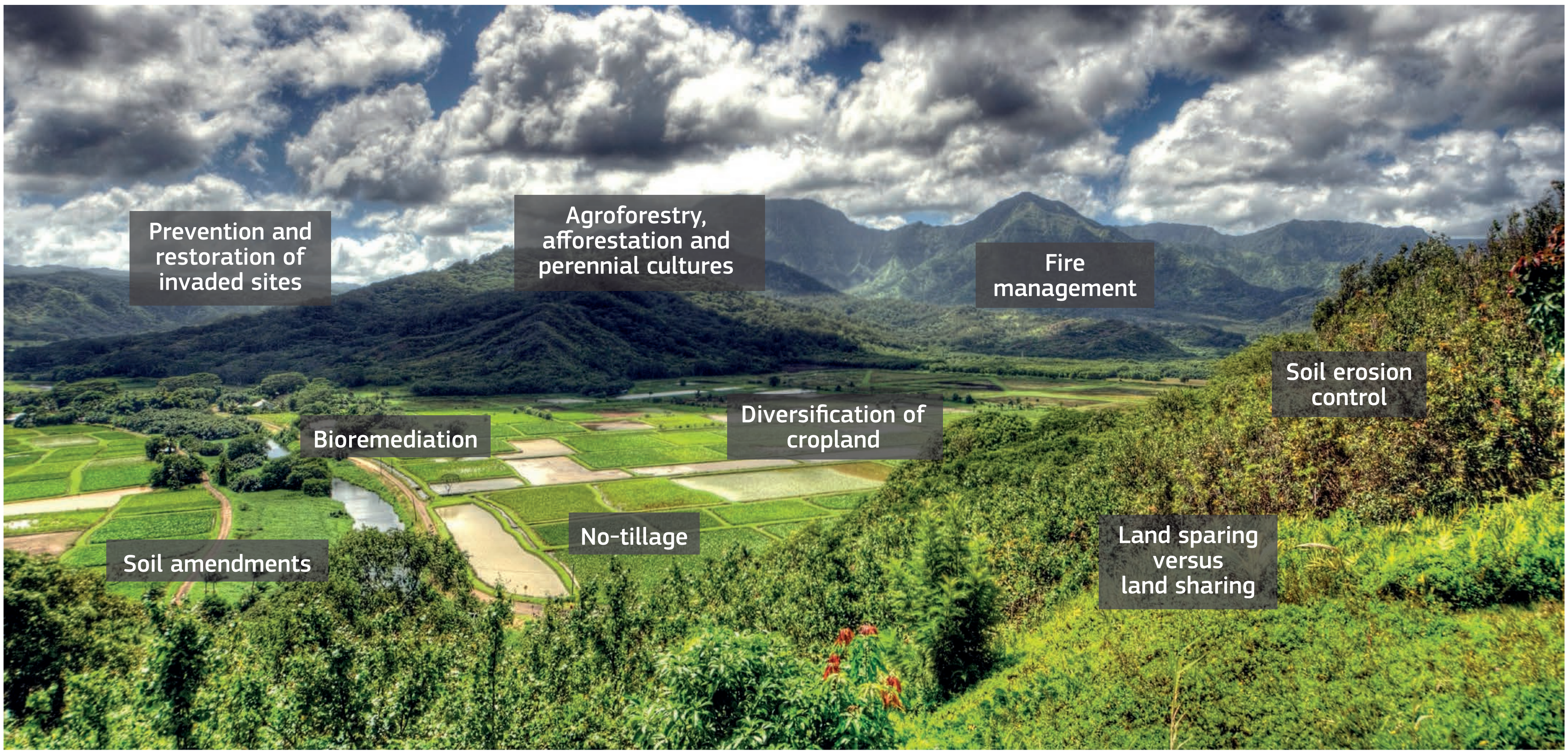
Conservation of soil biodiversity in agricultural landscapes is thus intrinsically linked to land use and management systems that conserve and promote soil niche diversity. Recent evidence has shown that there are strong links between aboveground biodiversity (vegetation/crops) and belowground biodiversity (soil organisms). This finding supports the concept that modifications in plant communities as a result of changes in land use and agricultural systems can have profound impacts on the niche diversity underpinning soil biodiversity. Furthermore, it highlights the great potential to strategically utilise land management systems to influence the provision of soil-mediated ecosystem services. Limited predictive understanding of plant-soil feedbacks, however, still constrains the ecological management of soil biodiversity.

In this section, we will explore different ways in which soil can be managed to conserve soil biodiversity and sustain soil-mediated ecosystem functions and services. We start with a broad discussion about 'land sparing' versus 'land sharing' as biodiversity conservation strategies. This is followed by efforts to address ecosystem restoration challenges associated with invasive species and pollution, as well as large impact systemic changes imposed by the diversification and perennialisation of agricultural landscapes. Next follows management practices that have been adopted with significant impacts on soil biodiversity, including no-tillage systems and fire management. We conclude with more specific management practices, such as erosion control measures, the application of biochar and other soil reconstruction methods.

What can we do to protect soil biodiversity?

- Support soil-friendly cultivation that minimises the use of chemical fertilisers or pesticides. Look for organic products in the supermarket.
- Try to provide opportunities to encourage soil biodiversity where you live. Leave parts of your garden unmanaged, allow branches and garden waste to rot naturally.
- Reduce your rubbish! Recycle where possible so that we minimise the chances of soil pollution.
- Think about your 'carbon footprint'. How are you contributing to global warming and climate change? Look at your energy consumption, try to use a bicycle or public transport instead of a car.
- Support woodland regeneration schemes.
- Encourage your local authorities to target new developments on brownfield sites so as to minimise their environmental impact. Limit, where possible, the sealing of surfaces by concrete or asphalt.
- Limit soil erosion, organic matter decline, compaction, salinisation and landslides, by identifying and communicating risk areas to land owners and local authorities.
- Carefully dispose of old medicines. Several pharmaceuticals can have significant impacts on organisms. Take old drugs to the pharmacy. Never flush them down the toilet.

We can contribute to soil biodiversity preservation through many simple actions, such as (**a**) supporting soil-friendly initiatives, (**b**) composting our organic rubbish and (**c**) preserving aboveground biodiversity and (**d**) natural predators to reduce the use of pesticides. (KTH, JGI, USMG/EBR, SFA)



There are several actions that can facilitate conservation of soil-living communities, which can be identified when looking at the environment around us. Most of the measures would be possible through a better management of human activities: from diversification of cropland to no-tillage and soil erosion control. (ARO, JRC)

Land sparing versus land sharing

Strategies for biodiversity conservation

Conserving biodiversity within networks of reserves from which intensive human activity is excluded is part of a strategy referred to as 'land sparing'. Consequently, agricultural land is presumably farmed more intensively for a higher yield, to reduce the area needed for production. [168]

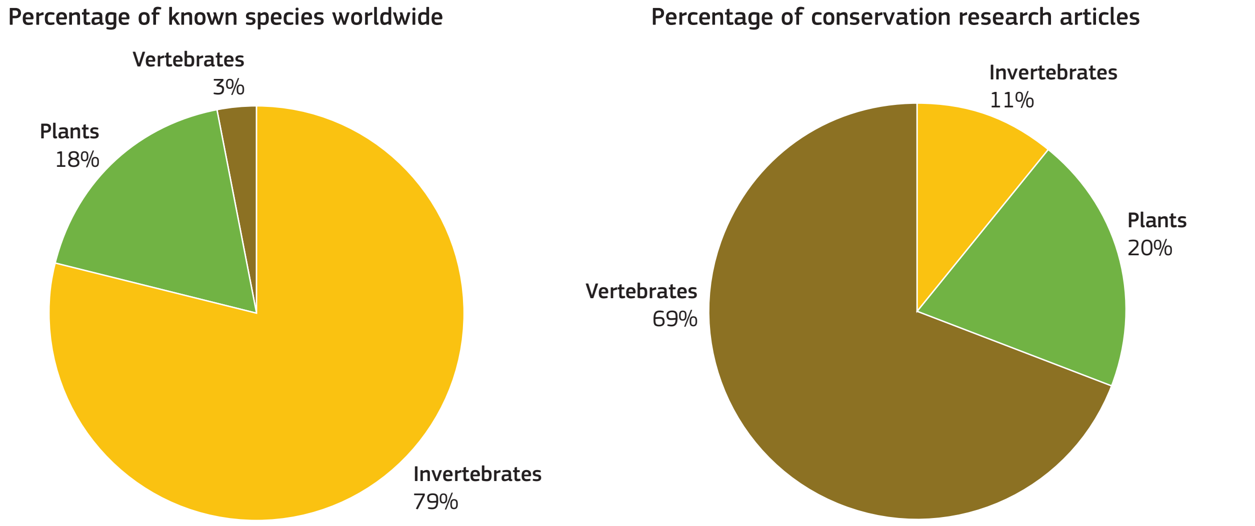
'Land sharing' means adopting wildlife-friendly practices to conserve biodiversity within a matrix of land uses, such as different levels of agricultural intensification, forestry, grazing and human settlements. Given that not all land can be taken out of production, systematic conservation planning focuses on 'sparing' areas that contain the greatest concentration and broadest representation possible of species, and which can be maintained as conservation reserves over the long-term.

Conservation planners often use vascular plants, mammals or birds as indicators of terrestrial biodiversity, as these are the taxa for which most data are available. Despite the fact that soil is likely to harbour the greatest concentration of terrestrial biodiversity, soil microorganisms and fauna have been almost completely ignored in conservation planning. Conservation research is systematically biased toward vertebrates, even though invertebrates represent nearly 80 % of known species.

Biodiversity hotspots

Relatively few studies have been carried out on the biogeography of soil biota (see Chapter III). From the limited evidence available, soil invertebrates, such as termites, ants, collembolans and earthworms (see Chapter II), appear to follow the same biogeographic patterns of species richness as aboveground species, such as an increase in species richness when moving from high latitudes to the Equator. However, soil microbes (e.g. bacteria and fungi – see pages 33-35, 38-41), nematodes (see pages 46-47) and oribatid mites (see page 49) do not seem to follow these patterns.

Soil microbes reach their greatest diversity in soils with neutral pH, which are more common in temperate climates than in the often acidic soils of the tropics. Ectomycorrhizal fungi (see page 40) are most diverse in boreal and temperate forest biomes, with reduced diversity in tropical forests. Nematode diversity is most closely linked to rainfall and temperature variables, and shows a weak latitudinal gradient. Oribatid mites increase in diversity from boreal to temperate regions, but there is no further increase in diversity toward the tropics.



(**a**) Proportion of major taxa in nature versus (**b**) proportion of articles in the conservation literature. In 2002, a study catalogued 2 700 original research articles published between 1987 and 2001 in two leading scientific journals on conservation (i.e. Conservation Biology and Biological Conservation). Most of the available research focuses on vertebrates (nearly 70 % of articles), even though invertebrates represent nearly 80 % of known species (derived from Clark and May, Science, 2002). (LJ, JRC) [171]

A recent molecular study suggested that there may even be an inverse relationship between aboveground and belowground biodiversity for some organisms. It has been suggested that areas highlighted for conservation attention due to their high vascular plant species richness may also be important for the conservation of soil macroinvertebrates.

Strong linkages between plant biodiversity and soil biodiversity have been increasingly recognised, including plant-soil feedbacks, and evidence of positive relationships between species richness of vegetation and soil-dwelling fauna, such as termites and oribatid mites. Conservation International has identified 35 global biodiversity 'hotspots' which contain at least 1 500 endemic vascular plant species, and for which 30 % or less of the original extent of vegetation remains. Plant biodiversity hotspots are concentrated in tropical and subtropical regions. Protecting these areas may be an important means to indirectly conserve soil biodiversity and the benefits provided to society by these organisms.

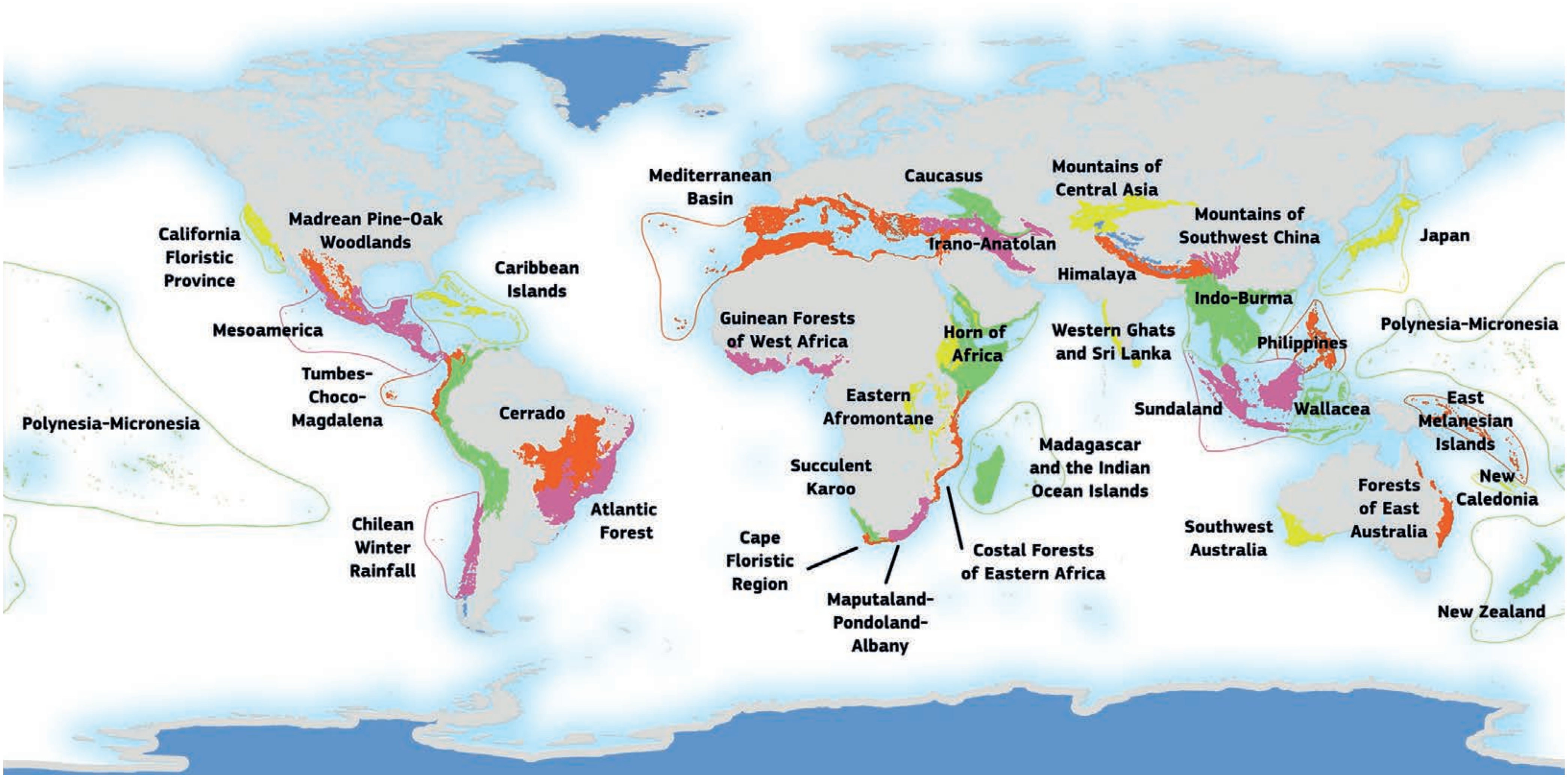
Soil biodiversity and reserve network

While numerous site-specific surveys and assessments have been completed around the world, it is difficult to draw clear conclusions about which parts of the world harbour the greatest concentrations of soil biodiversity.

One reason is that taxonomic knowledge of soil biota is far from complete, with the great majority of species undescribed. Biodiversity assessments tend to focus on particular taxa or groups of taxa, given the enormous task of systematically describing the complete suite of soil organisms present in any particular location.

Another contributing factor is that the species present in any particular location are often unique to that location; there are few truly cosmopolitan soil-dwelling species. This means that particular soils and vegetation types may have unique communities of microbes and invertebrates, making it difficult to single out specific, high diversity areas for priority conservation.

The adequacy of the existing reserve network to conserve soil biodiversity is unknown. The preservation of a representative suite of soil types in reserve networks, together with conservation management of undisturbed, unique and rare soils, are currently low priorities for environmental policy in most nations. Differences in soil type can explain a large proportion of variation in soil fungal and soil invertebrate diversity. There are indications that particular soils can have unique communities of soil biota, and that 'pedodiversity' (diversity of soil types in an area) is directly related to soil biodiversity, as well as aboveground biodiversity. Deliberate consideration of soil diversity in systematic conservation planning would assist in the conservation of soil biodiversity within the formal reserve network.



The 35 global plant biodiversity hotspots. Hotspots must contain at least 1 500 endemic vascular plant species. Protection of these plant species-rich areas may have positive impacts on the conservation of soil organisms (different colours aim at separating the hotspots). Data from Conservation International, 2011 (derived from Myers *et al.*, Nature, 2000 and Mittermeier *et al.*, 2005). (LJ, JRC) [169, 170]

Agriculture and biodiversity conservation

Due to the importance of soil biota to soil health and agroecosystem function, much of our knowledge about soil biodiversity comes from research conducted within agricultural areas. Many of these studies have concluded that high soil fauna biodiversity is supported by the heterogeneous nature of soils, and can be influenced over small spatial scales by different land-use practices and habitat variables (see Chapter III). While these studies may not be considered as 'conservation research' in the traditional sense, it is apparent that agricultural landscapes are actually very important habitats for a wide variety of soil microbes and invertebrate species.

Agriculture is the most significant and widespread form of human-environment interaction, consuming more natural resources than any other human activity. As the main driver of land conversion, biodiversity loss and changes in global biogeochemical cycles (see pages 104-105), the management of agricultural landscapes is increasingly important for biodiversity conservation. Human population growth and increasing demands for food, fuel and fibre mean that following a 'land sparing' approach alone is unlikely to achieve conservation goals.

The general consensus that soil spatial heterogeneity is largely responsible for the enormous biodiversity housed in soils highlights the importance of 'land sharing' approaches that foster habitat heterogeneity through diverse agricultural practices, which optimise rather than maximise the use of natural resources. Over time, both agricultural production and biodiversity conservation may take place within more integrated (rather than segregated) landscapes by following an approach that combines both land sparing and land sharing.

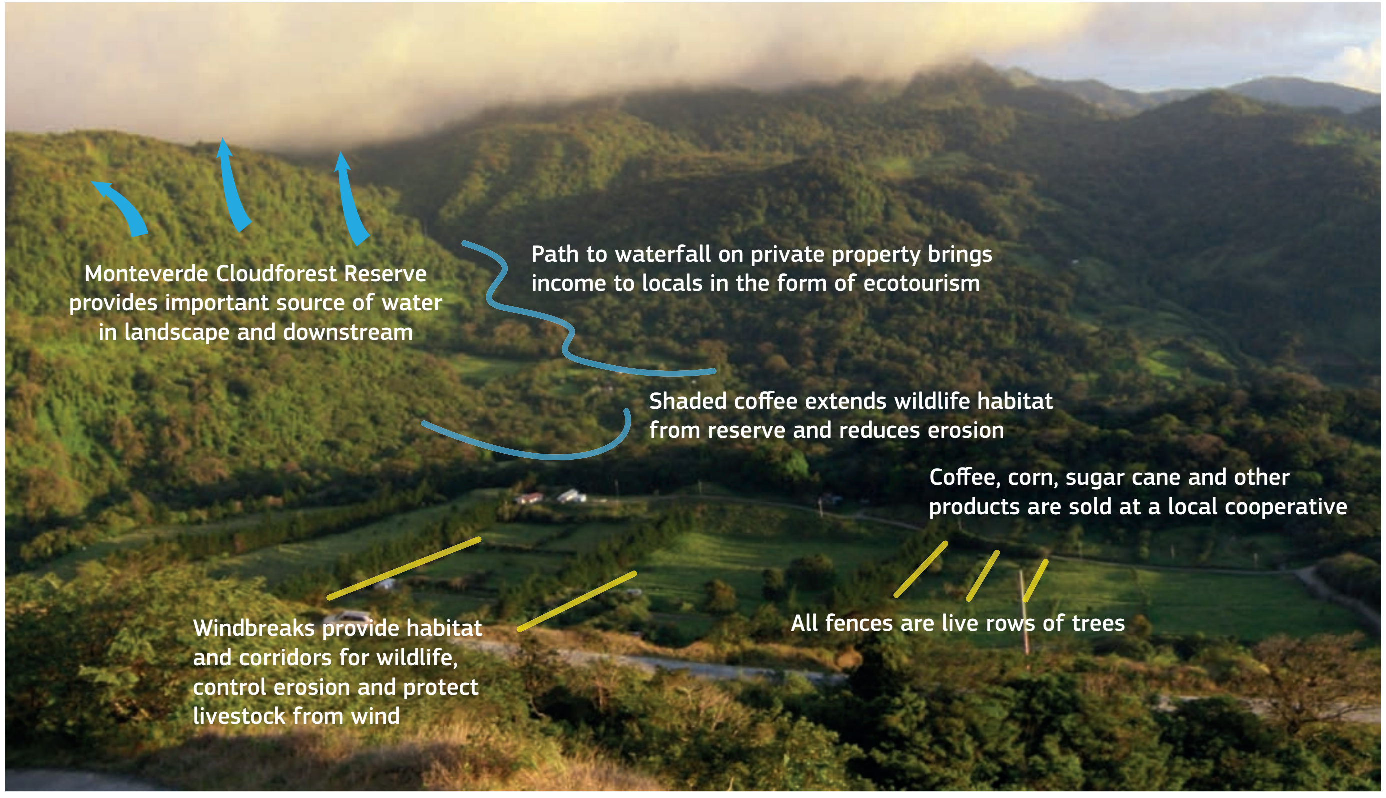
Examples of projects to preserve soil biodiversity

The Conservation and Sustainable Management of Belowground Biodiversity (BGBD) project selected benchmark sites that represent globally significant ecosystems and land uses. Many of the BGBD project sites coincided with Conservation International's plant biodiversity hotspots, including those in the Veracruz Biosphere Reserve in Mexico (Mesoamerican hotspot), the Ivory Coast (Guinean Forests of the West Africa hotspot), Kenya (within the Eastern Afromontane hotspot), in the Western Ghats and Himalayan hotspots in India, and Sumatra in Indonesia (Sundaland hotspot), as well as the Brazilian Amazon.

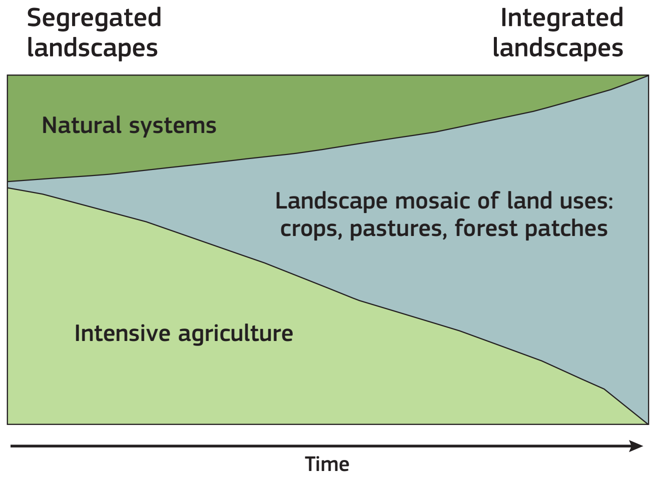
Soil organisms were sampled along gradients of agricultural intensification at each site, in order to determine the extent to which soil biodiversity conservation could be achieved in mosaic landscapes where sustainable agricultural production was an important goal. Additionally, the Alternative to Slash and Burn (ASB) Partnership for the Tropical Forest Margins assessed the relationship between agricultural land use and soil biodiversity in four benchmark sites, including the Brazilian Amazon, Cameroon (Congo Basin Rainforest), Sumatra and the Peruvian Amazon.

Examples of plant biodiversity hotspots: (**a**) rainforest in Sumatra and (**b**) succulent Karoo in South Africa. (ANH, CPR)

Results from the BGBD project showed that more intensive agriculture often leads to a decline in soil biodiversity. Mechanisms for this decline include a reduction in the amount and diversity of organic inputs into the soil food webs in more intensive agriculture (often by substituting with agrochemicals as the main source of nutrient input – see pages 122-123), and by modification of the soil microclimate. Furthermore, hydrological functions are affected after passing certain intensification thresholds, as reduced infiltration promotes increased runoff and soil erosion (see pages 128-129), resulting in a downward spiral of degradation. ASB studies returned mixed results. In some cases, agricultural intensification led to reduced diversity and changes in community structure, particularly for termites (see page 55), while in some sites there were no substantial changes, and some elements of the biota increased in abundance (such as mycorrhizal fungi and sometimes earthworms – see pages 40, 58). Their research also showed that agricultural diversification and proximity to forested zones can promote and sustain belowground biodiversity.



An example of an 'eco-agriculture landscape' (analogous to 'land sharing' approaches to biodiversity conservation) near the Monteverde Cloud Forest Reserve in Costa Rica, integrating farming and landscape considerations. Mosaic landscapes such as these offer a diverse habitat for a range of soil-dwelling species. (EPA/ND)



Likely land-use trajectories from segregated landscapes (i.e. land sparing), where different land uses are kept separate, to integrated landscapes (i.e. land sharing), where natural and agricultural systems are combined (derived from van Noordwijk *et al.*, Conservation Ecology, 2001). [172]

The 'land sharing' approach to conservation recognises that biodiversity can be conserved within mosaic landscapes, including agricultural land use. For many of the tropical biodiversity hotspots, the existing network of protected areas may be inadequate for protecting biodiversity, especially where refuges are small, isolated or poorly protected.

Protected areas

- The International Union for Conservation of Nature (IUCN) defines a protected area as 'a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values'. [173]
- The 2014 United Nations List of Protected Areas contains 209 429 protected areas covering a total area of more than 30 million km^2 – an area larger than the African continent.
- In total, 14 % of the world's terrestrial areas are currently protected.
- The IUCN set categories that provide international standards for defining protected areas and encouraging conservation planning according to their management aims:
  - category Ia — strict nature reserve;
  - category Ib — wilderness Area;
  - category II — national Park;
  - category III — natural monument or feature;
  - category IV — habitat/species management area;
  - category V — protected landscape/seascape;
  - category VI — protected area with sustainable use of natural resources.

There are more than 5 000 national parks on our planet. Here is the Killarney National Park in Ireland. (JMR)

However, agricultural areas can make an important contribution to overall conservation objectives, particularly where land use is heterogeneous (including patches of native vegetation where species sensitive to disturbance can shelter, and which can act as 'source zones' for recolonisation), and agricultural areas include a taxonomically, structurally and functionally diverse range of plants. The following sections outline some of the ways in which land use and management practices can be used to preserve soil biodiversity.

Prevention and restoration of invaded sites

Benefits of soil biodiversity

Soils associated with indigenous plants tend to have a higher number of specialist organisms, such as host-specific pathogens, or nematodes (see pages 46-47) that feed on certain root types, but also specialist beneficial (micro-)organisms (e.g. mycorrhizal fungi – see page 40). With the introduction of invasive plants, the species composition of these soils shift to contain more generalist species (see page 118). An example of this shift in species composition is noted with the increased levels of mycorrhizal and decomposer fungi beneath stands of invasive species, and a decline in the number of host-specific pathogenic fungi, which ultimately impacts on aboveground diversity. The build-up of dead plant biomass in the soil provides a greater amount of substrate for the decomposers. However, it is not only an increased diversity of decomposer species that have been noted. [174]

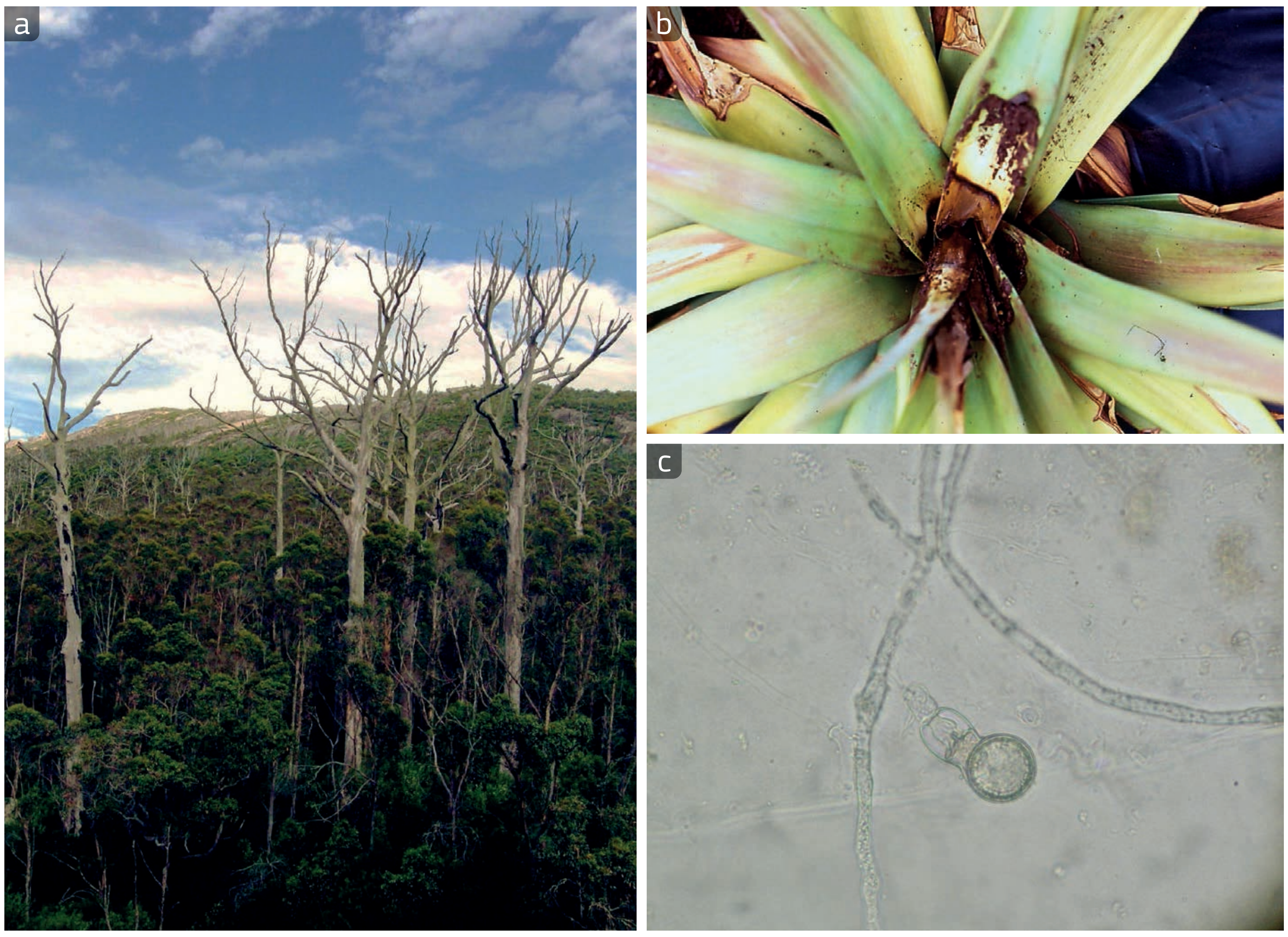
It has also been reported that the diversity of nitrogen-fixing soil bacteria species (symbiotic and non-symbiotic – see box on page 33) associated with the roots of invasive species, increased significantly in comparison to soils under native vegetation. The resulting increase in soil nitrogen not only contributes to sustaining the high growth rates of the invasive species, but also of other soil organisms. Studies have shown a strong correlation between increased soil nitrogen beneath stands of invasive tree species and increases in the diversity of earthworm species (see page 58). These changes, however, are often at the expense of the indigenous soil fauna and flora which were better adapted to the soil conditions that existed prior to the introduction of invasive species.

Early warning

Despite the partially positive effects reported above, the introduction of alien species is generally considered to be a serious threat. The impact of an invasive species on native species and on ecosystem functioning depends on the new species' diet, speed of reproduction and spread, and the cascading effects caused. A well-known example of a devastating invasive species from both an ecological and an economic perspective is the pathogenic protist (see pages 36-37) *Phytophthora cinnamomi*, which caused mortality in at least 900 tree species, including many fruit trees, chestnuts, walnuts and ornamental species. The symptoms of *P. cinnamomi* infection are wilting, foliage desiccation and root necrosis. The native range of *P. cinnamomi* is Southeast Asia; however, it was accidentally introduced and has spread in Australasia-Pacific, Europe, North America and South Africa through the (international) transport of infected soil and/or roots.

The plant (**a**) *Prosopis juliflora* is native to South America but has become an invasive weed in Africa where (**b**) it is invading farms. (FKS, TFTF)

Prevention is the most effective management strategy to combat invasive species given the high economic costs and logistical efforts required for chemical control, physical removal of invasive species, and restoration through habitat rehabilitation and replanting. Early-warning and rapid-response frameworks have been put forward to control the proliferation of invasive species. These involve surveillance, early detection (DNA-based identification – see pages 64-65) and monitoring approaches, supported by species databases, inventories and expert registries that have led to the definition of 'black', 'watch' and 'alert' lists. In this regard, the Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN) runs the Global Invasive Species Database which provides information on invasive species, such as year and pathway of introduction, specific impacts in the places of introduction and possible management options.



(**a**) Eucalypts killed by a disease known as dieback in an Australian forest in Western Australia. (**b**) The same disease affects pineapple plants in Hawaii. The agent responsible for this disease is the invasive soil protist (**c**) *Phytophthora cinnamomi*. The geographical origin of *P. cinnamomi* is not clearly established, even though it was first described in Indonesia (Sumatra). (IGE, SCN, NNG)

Removal of invasive species

After the removal of invasive species from an ecosystem, the time since the start of the invasion remains one of the key factors in determining if, and how, the ecosystem will return to its original state. The longer the soils were exposed to the invasive species, the greater the changes that would have taken place in terms of soil chemistry and soil communities and, consequently, the longer it will take for these soils to return to resembling their natural state.

Initially, changes will occur within the microbial communities, as organisms, such as bacteria and fungi, can persist in an inactive state in soil for long periods of time, becoming active only when conditions are favourable. However, changes within the communities of soil meso- and macroorganisms will be slower. Furthermore, allelochemicals (toxic chemicals produced by a plant in order to defend itself) that limit the action of specialist organisms (e.g. certain pathogens or specialist root-feeders) are likely to persist for some time after the removal of invasive plant species, although, it can be expected that these chemicals will be degraded or leached from the soils over time.

(**a**) Seeds of (**b**) *Acacia saligna*. This plant has become invasive in Australia. After clearing an area of invasive plants, the large seedbanks and soils that have been primed for the establishment and support of invasive plants are reasons for the need to continue monitoring cleared areas for a number of seasons post clearing, in order to prevent the re-establishment of the invasive plants. (TSL/USDA, SOA)

As the aboveground vegetation changes from invasive to indigenous species, the input of large amounts of biomass to the soil will diminish, providing less substrate to support the large communities of decomposers, and slowing down the nutrient-cycling processes. It can be expected that, to a certain extent, the niche diversity of these ecosystems will be restored upon removal of the invasive plant species, but this process will take time and is dependent on the management of aboveground species and inputs, such as restoration planting or herbicide use. Furthermore, the removal of invasive plant species will leave soils that are well suited for the re-establishment of invasive plants, thus requiring careful management and revegetation with indigenous species.

The monitoring of these areas, and removal of any newly germinated invasive plants, should continue for a number of years after revegetation by the native plants has taken place. This is necessary as, for a number of years after the original stand of invasive species has been removed, the soil environment will continue to favour the establishment of invasive plants and, as a result, they would still have a greater competitive advantage over the indigenous species.

Bioremediation

Soil biodiversity for bioremediation

Without doubt, the best way of managing soil pollution is to prevent it from happening and to regulate the management of waste and the use of pesticides. Over the past decades, growing awareness of environmental impacts has led to regulations on the use of old, often dangerous, substances and the development of new pesticides based on thorough testing of their side-effects on soil life (especially earthworms, enchytraeids and collembolans – see Chapter II). [175]

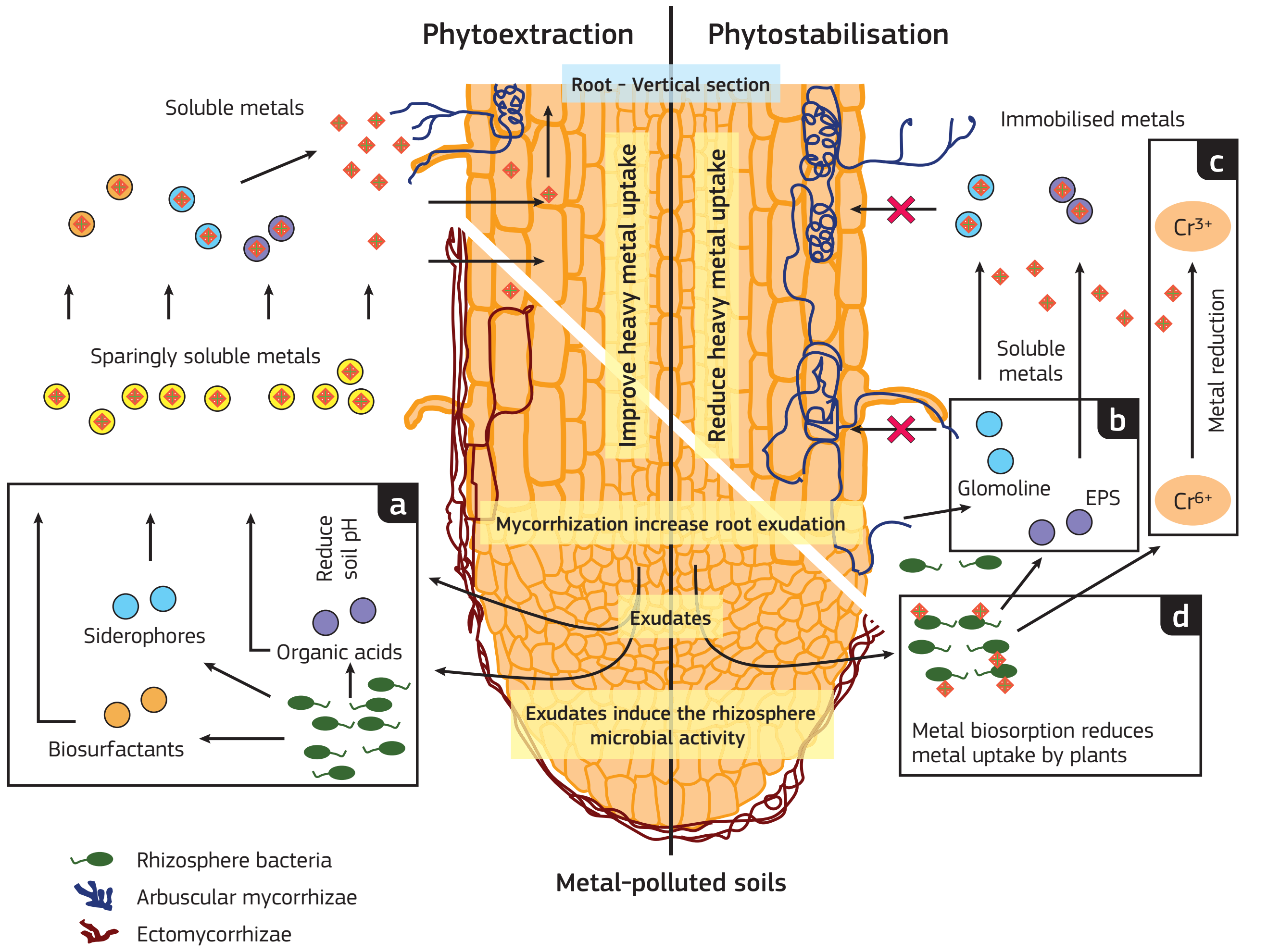
In the unfortunate cases where soil pollution occurs (see page 120), soil biodiversity can be of great help through the cleaning services it provides in the form of bioremediation agents (see page 100). Notably of organic compounds can be degraded through the use of specific species of soil bacteria and fungi. These species can be inoculated into the polluted areas or, if they are already present in the soil, their activity can be stimulated. For example, the capacity of the wood decomposer fungus *Pleurotus ostreatus* (also commercially known as the oyster mushroom) to remove polycyclic aromatic hydrocarbons (PAHs) from a highly contaminated soil was tested. After a 12-week treatment period, a reduction in PAHs of 50 % up to about 90 % was observed, demonstrating the PAH-removal potential of the oyster mushroom.

The oyster mushroom (*Pleurotus ostreatus*) has great bioremediation potential due to its capacity to absorb pollutants from contaminated soils. In nature it can be found in forests, where it decomposes dead wood, especially deciduous trees. (TSC)

When bioremediation is carried out by plants (phytoremediation), specific groups of soil bacteria and fungi (see pages 33-35, 38-41) can help to increase speed and/or efficiency. For example, the bacterium *Ralstonia metallidurans* carries out bioremediation of heavy metals in soil. The mechanisms by which soil bacteria and fungi help plants through bioremediation are dependent on the species of bacteria and fungi and their metabolic potential. There are two pathways for phytoremediation; the first considers less direct action by soil organisms, whereas the second is more based on soil biota.

The first mechanism, known as 'phytoextraction', in which plants play the main role, involves the use of metal-accumulating species to remove metals from soil by concentrating them in the harvestable parts of the plant. However, in order to be accumulated by plants, heavy metals must be made available. Soil organisms act at this stage by increasing the solubility of heavy metals and, thus, their uptake by plants. Once plants have absorbed the pollutants, they can be harvested. The plant material may need further treatment to concentrate and possibly recycle the pollutants, otherwise it can be incinerated.

The white lupin (*Lupinus albus*) shows phytostabilisation abilities by reducing the soluble cadmium fraction in soil. (DSP)



Plant-associated microbes accelerate the phytoremediation process in metal-contaminated soils by enhancing metal mobilisation/immobilisation. Mobilisation processes allow for phytoextraction (i.e. plant roots absorb heavy metals from soil). (**a**) Plant-associated microbes contribute to this process by producing metal-mobilising substances, such as siderophores, biosurfactants and organic acids. Immobilisation processes lead to phytostabilisation (i.e. metals remain in the soil but are transformed into harmless forms). Plant-associated microbes contribute to this through (**b**) the production of metal-immobilising extracellular polymeric substances (EPS) or others (e.g. glomalin), (**c**) metal reduction and/or (**d**) metal biosorption (i.e. direct absorption into microbial cells – derived from Rajkumar *et al.*, Biotechnology Advances, 2012). [176]

What are heavy metals?

- At first glance, it would appear to be a rather simple matter to define a 'heavy metal': it is a metal that is 'heavy'. Unfortunately, a more in-depth consideration reveals a huge amount of problems with this simple definition.
- Regarding their role in biological systems, heavy metals are classified as essential and non-essential. Essential heavy metals are those needed by living organisms in minute quantities for vital physiological functions. Examples of essential heavy metals are iron, manganese, copper, zinc and nickel. Non-essential heavy metals are those not needed by living organisms for any physiological functions. Examples of non-essential heavy metals are cadmium, lead, silver, mercury and chrome.
- The term 'heavy metal' is linked in many people's minds to metals (or their compounds) that are toxic. However, this is a feeling rather than a conclusion based on scientific evidence. A heavy metal is not toxic *per se*; it is only toxic when its concentration exceeds a certain threshold. With regard to soil, we are generally concerned with toxicity to plants. In this context, the main heavy metals are: cadmium, mercury, copper, nickel, zinc, chrome, arsenic and lead.
- Agricultural soils in many parts of the world are slightly to moderately contaminated by heavy metals. This could be due to long-term use of fertilisers, sewage sludge application, industrial waste and unsuitable irrigation practices in agricultural lands.

The second mechanism is known as 'phytostabilisation'. Phytostabilisation is the most successful and well acknowledged process of phytoremediation. In this case, plants provide a suitable zone around their roots where the pollutants can be stabilised and immobilised by soil organisms. Consequently, in this process the contribution of soil biota is more evident. In particular, heavy metals are rendered harmless by soil microorganisms through different mechanisms, such as the production of specific substances (e.g. glomalin produced by arbuscular mycorrhizal fungi) that immobilise metals, the direct absorption by microbial cells and the direct reduction of heavy metal.

The process that facilitates identification of species suitable for bioremediation often requires a long time and several experiments to test the efficiency and applicability of the selected organisms at large scale. Nonetheless, current scientific knowledge shows that the use of soil organisms for bioremediation is feasible and recommended.

Soil biodiversity as a bioindicator

The abundance and diversity of soil organisms in unpolluted healthy soils are high, while in polluted soils a marked decline in abundance and species richness of soil biota occurs. In particular, slow growing and highly sensitive species (e.g. some fungal species) are the first to disappear from the soil communities. The targeted organisms and effects depend on the type of pollutants. Therefore, the composition of the soil communities can be indicative of the level and type of pollution, and soil organisms can be used as bioindicators (see page 101) of soil pollution.

Nematodes do not rapidly migrate away from stressful conditions. As a result, the community structure is indicative of conditions in the soil that it inhabits. (SCN)

Nematode communities (see pages 46-47) have been used for this purpose as the ecology and sensitivity to disturbance of many species in this widely distributed group of soil organisms is well established. Based on the species composition of nematodes, indices of disturbance can be calculated (e.g. Maturity Index) and used to assess the severity of the pollution not only for the nematodes but also for the structure and functioning of the whole soil food web (see page 96). In fact, each nematode family can be classified into a coloniser-persister (cp) scale. The scale ranges from one (early colonisers of new resources) to five (persisters in undisturbed habitats). The maturity index (MI) of soil is the weighted mean cp value of the individuals in a representative soil sample. In practice, low MI values indicate a disturbed and/or enriched environment, high MI values indicate a stable environment. By calculating this index, it is possible to carry out a preliminary assessment of the state of health of a given environment.

Diversification of cropland

Same time, same place, different crops

Agricultural intensification associated with the 'Green Revolution' led to a dramatic simplification of cropping systems throughout the past century. Farmers, once reliant on complex associations of crops and livestock to manage pests and soil fertility across relatively small areas, now more typically manage vast expanses of farmland dominated by a single crop, and are largely dependent on agrochemical inputs to control the growth environment of the crop (see pages 122-123). While the shift to large-scale monoculture cropping systems has served to dramatically increase crop yields, this form of management has been shown to have deleterious impacts on biodiversity at both plot and landscape scales. [177]

Interest in the diversification of agroecosystems is growing and enhanced complexity of the crop species managed is seen as an important strategy for addressing issues of long-term agricultural sustainability, soil biodiversity conservation and resilience in the face of global change and growing demands on agriculture. Polyculture is one way of diversifying agriculture at the plot scale to enhance overall productivity and/or the provision of key ecosystem services (see Chapter IV) through:

- the intermixing of different crops, such as the row intercropping system (the cultivation of two or more crops simultaneously on the same field in a row arrangement) and relay cropping (two or more crops on the same field with the planting of the second crop after the first one has completed its development)
- the combination of crops with beneficial plants, such as the companion planting system (the planting of different crops close to those of interest for pest control, pollination or providing habitat for beneficial creatures) and trap crops (species that attract agricultural pests, usually insects, away from nearby crops)

Examples of intercropping systems: (**a**) wheat-fava in China and (**b**) tomato-coffee in Colombia. (CWF, NP/CIAT)

In addition to the abovementioned benefits, there are a number of mechanisms by which increasing spatial and temporal diversity can help support biological activity and diversity in soils. However, relatively little research to date has examined the impact of such agroecosystem diversification on belowground biodiversity and functioning. The polyculture systems discussed in this section focus on crop diversification, which differs from agroforestry, and diversification by the inclusion of trees in cropland areas (see pages 144-145).

Effects of polyculture on soil biodiversity

While the management of polycultures can be different from that of monocultures in a number of ways, the most salient feature is the intentional commingling of multiple plant species in space. To date, research examining the impact of plant diversity on soil communities has yielded somewhat mixed results, yet there exists a general trend suggesting that increasing plant community complexity enhances the biodiversity of soils (see page 118). The exact nature of this effect, however, appears to depend on the ecological context and the taxonomic or functional groups in question, thus suggesting that polycultural impacts on belowground biodiversity are likely to vary. For example, the abundance and diversity of organisms that are intimately associated with plant roots (e.g. mycorrhizal fungi – see page 40) typically show more immediate responses to increases in plant diversity. Meanwhile, decomposer biota more often demonstrate legacy effects, whereby alterations to belowground community structures reflect longer-term shifts in soil organic matter quality and quantity following the transition from monoculture to polyculture systems. It has also been shown that plant diversity impacts on soil biodiversity tend to increase over time, regardless of functional group. This implies that the implementation of polycultures that are frequently disturbed (i.e. those based on annual crops and recurrent tillage) may benefit belowground biodiversity less so than in perennial systems that are based on trees or semi-permanent pastures.

The potential impacts of polyculture on belowground biodiversity mentioned above are likely due, in part, to increased resource heterogeneity in the soil. Greater complexity in plant community architecture, rooting patterns (see page 43), litter chemistry (see page 106), and root exudation, among other factors that are associated with increasing plant diversity, allows for greater niche diversification (e.g. available microhabitats and nutritional resources) and can alter belowground species interactions to enhance overall soil biodiversity. For example, it has been clearly shown that diversity in the quality and quantity of root exudates can impact the diversity and abundance of rhizosphere microorganisms. Furthermore, plant species mixtures often exhibit greater productivity than monocultures and, subsequently, enhance the flow of energy to the soil subsystem in the form of greater aboveground residues and rhizosphere inputs. This augmented resource base offers another means by which polycultures can support larger and more diverse soil communities. This is most evident when distinct plant functional groups are combined to enhance overall resources.

This home garden in Ghana is an extreme example of polyculture with over 10 different crops grown within a radius of several metres. (SJF)

While plant diversity in and of itself (e.g. total species richness) has been demonstrated to be an important driver of soil communities, the inclusion of certain plant species can have disproportionate impacts on belowground activity and diversity. Nitrogen-fixing legumes offer a clear example of a plant functional group that can have long-lasting and cascading effects on soil communities. For example, legumes often enhance earthworm populations due to the improved nutritional quality of organic matter inputs. The promotion of these ecosystem engineers (see box on page 95) has, in turn, been shown to dramatically enhance habitat complexity and the diversity of smaller organisms in soils due to macropores and biogenic aggregates, and complete restructuring of soil profiles (see pages 110-112). Other plant functional groups, such as grasses or woody species, can have similar impacts on belowground communities and should receive special consideration in the design and evaluation of agroecosystem diversification schemes. Therefore, while maximising plant diversity within polycultures may be a valid goal for some agroecological contexts, the inclusion of just one or a few additional plant functional groups within cropping systems is often sufficient and a much more feasible option for significantly enhancing soil biodiversity and functioning.

A general trend suggests that increasing plant community complexity enhances biodiversity in soils. (EBR/USMG)

Cover crops and soil communities

Cover crops, green manures and catch crops refer to farming practices where plants are not grown to be harvested but rather to help maintain soil productivity and fertility. The integration of these crops into a cropping system by relay cropping, overseeding, interseeding and double cropping represents a time-tested method that farmers have employed primarily to reduce soil erosion, increase soil organic matter content and nitrogen (N) availability to succeeding crops, control pests and to retrieve available nutrients from the system following a cash crop (i.e. grown for sale to return a profit). The terms 'cover crop', 'green manure' and 'catch crop' are often used interchangeably because they are usually grown to achieve more than one of the goals mentioned above. Here, we will use the term cover crop to refer to this practice.

The addition of cover crops, as mixtures or as individual species, to existing cash crops within cropping systems, can have many impacts on soil biota, both directly and indirectly. The inclusion of cover crops typically increases the spatial and/or temporal diversity of a cropping system, which can contribute a wide variety of residues and diverse root systems to support soil biota. Cover crop rhizosphere processes are a major source of carbon (C) and nitrogen (N) input to the soil, and microorganisms (e.g. bacteria) preferentially colonise the rhizosphere to access these nutrients. The increased contribution of C by the roots of cover crop also improves soil structure and aggregation, thereby creating a mosaic of microhabitats, whose chemical and physical properties may contribute to the heterogeneous distribution of microorganisms and their activities, and interactions among soil aggregates of different sizes. Qualitative differences among nutrient inputs, in the form of exudates (high C:N ratio – see page 106), belowground biomass (range of C:N ratio) and incorporated aboveground material (higher C:N ratio) associated with cover crop inputs govern microbial abundance, diversity, and activity (e.g. respiration and N mineralisation – see page 105). These differences may subsequently create a uniquely diverse and active microbial community necessary to decompose and process this mélange of inputs. The variety of inputs combined with the associated changes in microbial communities is also likely to have impacts on other decomposer organisms and higher trophic groups.

Besides increasing the amount of resources entering a system, increased plant diversity can also enhance the stability of plant-derived resources of belowground communities by ensuring greater continuity of plant residue inputs over time. This is clearly demonstrated in agroforestry systems (see pages 144-145) where perennial plant components are integrated into annual cropping systems, thus offering both food and other resources to soil biota during the 'off' season, when crops are absent or inactive due to drought or cold. Similarly, cover crop management can allow for residue cover and living and decomposing roots to be present in the soil potentially throughout the year. Compared to monocultural systems (see page 123), long-term (> 10 years) crop rotations that include legume cover crops have shown greater soil faunal and microbial activity that could lead to a differentiation in N cycling and storage. For example, the annual cover cropping and manure amendments characteristic of organic cropping systems have been shown to produce a more abundant, active, compositionally diverse and resilient community of soil microorganisms and its associated soil health benefits.

Earthworm-worked soil with greatly modified soil pores and biogenic structures create a diverse range of habitats for smaller soil organisms. (SJF)

Cover crop seedlings coming up in soil with a wheat stubble residue cover in South Dakota (USA). (CKE/USDA)

Crop value and production

- A crop is any cultivated plant that is harvested for food, clothing, livestock fodder, (bio)fuel, medicine or other uses.
- The United Nations Food and Agriculture Organization (FAO) calculates the annual values and production of crops cultivated by the countries of the world. [178]
- The value and production of individual crops vary substantially from year to year as global prices fluctuate. Country markets, weather and other factors influence production.
- In 2012, the most recent year with available data, the ten most valuable crops globally were:
  1. rice (~ US$187 thousand million – approx. €174 G);
  2. wheat (~ US$79 thousand million – approx. €74 G);
  3. soybeans (~ US$61 thousand million– approx. €57 G);
  4. tomatoes (~ US$59 thousand million – approx. €55 G);
  5. sugar cane (~ US$58 thousand million – approx. €54 G);
  6. maize (~ US$54 thousand million – approx. €50 G);
  7. potatoes (~ US$49 thousand million – approx. €46 G);
  8. fresh vegetables (~ US$46 thousand million – approx. €43 G);
  9. grapes (~ US$38 thousand million – approx. €35 G);
  10. cotton (~ US$37 thousand million – approx. €34 G).
- Considering the global production, the ranking is:
  1. sugar cane (~ 1 800 thousand tonnes);
  2. maize (~ 873 thousand);
  3. rice (~ 738 thousand);
  4. wheat (~ 671 thousand);
  5. potatoes (~ 365 thousand);
  6. fresh Vegetables (~ 270 thousand);
  7. sugar beet (~ 270 thousand);
  8. cassava (~ 269 thousand);
  9. soybeans (~ 241 thousand);
  10. tomatoes (~ 162 thousand).

Sugar cane is the crop with the highest production (in tonnes) at global scale and the fifth in terms of economic value. (FF)

Indirect impacts on soil communities

Beyond the relatively straightforward mechanisms described above, a number of indirect and inherently more complex phenomena within polycultural systems are likely to influence soil communities. For example, polycultures have demonstrated clear benefits for aboveground diversity and food web structure (see page 96), compared to monocultures with the same crops. In particular, the promotion of predators and biocontrol agents (see page 109) is an often-cited objective of polycultural management. While often overlooked, population increases in aboveground predators have been shown to yield important consequences for belowground, non-target fauna that often serve as supplementary food sources. Plant diversity impacts on other aboveground groups (e.g. herbivores) can have similar effects on soil communities. While such phenomena may represent major drivers of soil biodiversity in some ecosystems, they remain poorly understood and difficult to predict or manage.

Associated management impacts

While the above section discusses the direct and indirect impacts of increased plant community complexity on belowground biodiversity, such modifications to agroecosystems are often associated with other management practices that differ markedly from monocultures and can have important impacts on soil communities. For example, polycultures are often designed to reduce dependence on agrochemical inputs and tillage (see pages 122-123), which can represent important disturbances to soils and soil communities. This is perhaps most important in the case of pest management.

Pesticides can have strong impacts on both above- and belowground communities and have been shown to reduce soil biodiversity and food web complexity, via direct and indirect impacts on multiple taxonomic groups. In this regard, there is growing interest in the use of *Brassica* and mustard cover crops for their 'biofumigation' characteristics, as they have been shown to release biotoxic chemicals during decomposition that can reduce disease, weed and nematode pressure on the subsequent crop. While such biofumigation may have mixed effects for belowground biodiversity in the short-term, increased resource heterogeneity and enhanced productivity of the subsequent crop are likely to help promote overall biodiversity in the long run.

The application of inorganic fertilisers is perhaps less noxious than pesticides to many soil organisms, but these inputs can have deleterious impacts on some soil groups, particularly when applied in excess. Although tillage reduction is not commonly associated with polycultures and cover crop management, this feature is important for some forms of agroecosystem diversification (e.g. agroforestry and emerging no-till cover crop systems – see pages 144-147) and can dramatically alter belowground community structure and function. While other aspects of (agro)ecosystem management may be more important for promoting and/or conserving soil biodiversity, enhancing plant species diversity (both spatially and temporally) offers an important means to both directly and indirectly influence belowground soil communities.

Agroforestry, afforestation and reforestation

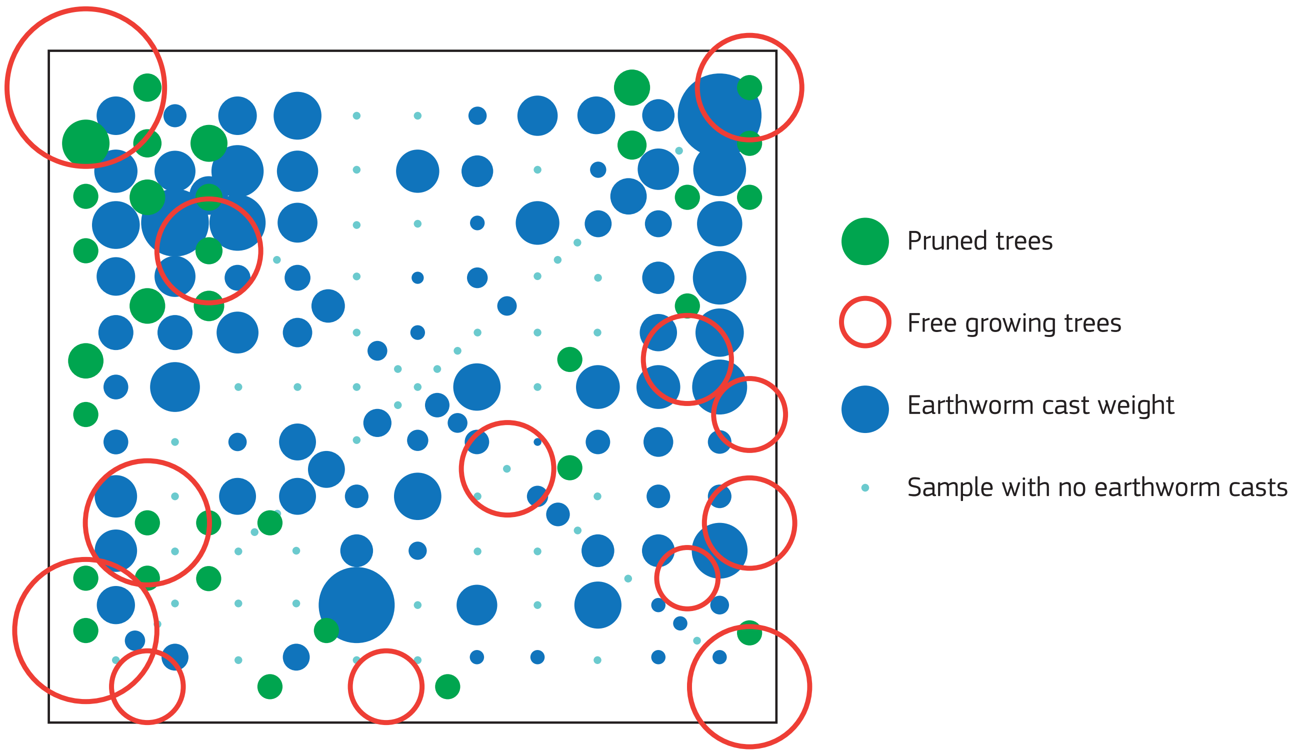
Planting trees

Agroforestry is a land use practice that combines trees with crops and/or animals, arranged in space or following a temporal sequence, and benefits from ecological interactions between trees and agricultural components. Agroforestry has been increasingly recognised and practiced as a land management option that can simultaneously contribute to income, food security and the conservation of biodiversity and ecosystem services. Furthermore, it is also considered a climate change mitigation and adaptation tool for agriculture. [179]

Afforestation and reforestation both refer to establishment of trees on land without trees. Reforestation refers to establishment of forest on land that had recent tree cover, whereas afforestation refers to land that has been without forest for much longer. These practices are used by landholders who want to plant and maintain a forest on their land to, for example, minimise erosion, reduce salinity or improve water quality.

Both agroforestry and afforestation/reforestation can be considered as effective measures to counter deforestation and the consequent loss of aboveground biodiversity that negatively impacts soil life (see page 118).

Examples of agroforestry: (**a**) trees of *Faidherbia albida* in cropping fields in Tanzania; (**b**) the legume *Gliricidia* with maize in Zambia; (**c**) seedlings of teak (*Tectona* sp.) and rice in India. (ICRAF)



Spatial distribution of soil biological activity near agroforestry trees (size of blue circles represents earthworm cast weight as a measure of biological activity). Earthworm activity is greater near trees (derived from Pauli *et al.*, Pedobiologia, 2010). [180]

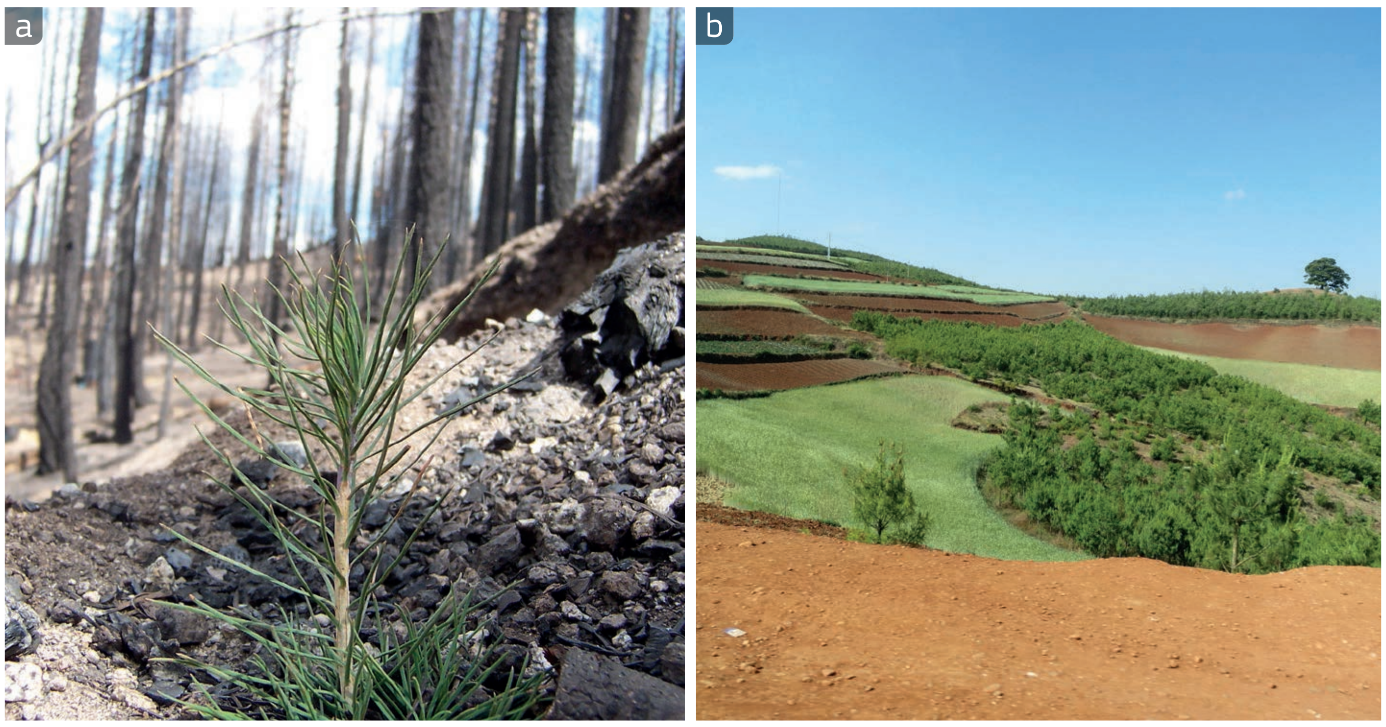
Effects on soil biodiversity

The integration of trees into landscapes has the potential to generate a number of improvements in the soil as a habitat for soil organisms. Trees promote changes in the soil environment in many ways; the tree canopy intercepts rainfall and provides shade to the understory and soil, and dead or pruned leaves and branches provide soil cover, as well as organic matter and nutrient inputs to soils (see page 17).

Periodic pruning of native trees followed by mulching in dry and sub-humid tropical environments allows for the maintenance of an organic layer on the soil, thus minimising soil erosion, helping to lower soil temperatures, and reducing water losses through evapotranspiration. In addition, the organic layer supports higher soil moisture levels required for the survival and activity of soil organisms, particularly during the dry season. Furthermore, mulch biomass is also a source of carbon and nutrients required for soil biological activity.

The key 'refuge' role played by trees in fostering favourable conditions for increased abundance of soil biota in their area of influence has encouraged their recognition as 'hotspots' of soil biological activity that contribute toward functional resilience (see page 97). Furthermore, recent agroforestry studies have shown that the distribution of soil biological activity was closely related to the spatial arrangement of trees, and that this effect was more pronounced for some tree species than others.

Pruned *Erythrina poeppigiana* trees used in shade coffee systems in Costa Rica. (PVA)



(**a**) A tree seedling planted in a burnt forest for a reforestation project in the USA. (**b**) Trees planted for an afforestation project in China. Reforestation and afforestation are a land-use change from non-forest to forest land through planting; the methods differ only in that afforested lands may not have contained forest previously. (USFS, LPU/CIFOR)

Trees as 'resource islands'

The concept of 'resource islands', analogous to that of trees as hotspots of soil biological activity, has emerged in semi-arid regions of Africa as a result of studies of the native shrubs *Guiera senegalensis* and *Piliostigma reticulatum* as key components of farmer-managed natural regeneration efforts contributing toward afforestation. These shrubs have tap roots that reach wet subsoils near the water table and are able to transfer water from deeper soil layers to the rhizosphere (see page 43) that is close to the soil surface through a process known as 'hydraulic lift'. This finding has changed the paradigm of how ecosystems can function under severe water limitations.

Previously, it was thought that biologically driven soil processes would largely stop during the dry season. Because of hydraulic lift, the diversity and activity of microbial communities (e.g. bacteria – see pages 33-35) can be maintained in the shrub rhizosphere during the dry season. By favouring conditions of resource availability (e.g. water), the trees create an island effect. These results obviously have implications for plant-microbial interactions related to biogeochemical processes, such as organic matter decomposition and nutrient mineralisation (see page 106). Research has also shown that the presence of *G. senegalensis* significantly increases crop yields of intercropped peanut and millet. This is partly due to improved water retention, and shrubs may assist crops through drought periods (a common occurrence during the growing season in the Sahel). Furthermore, such shrubs could also assist adjacent crops by promoting and harbouring beneficial microorganisms and suppressing plant pathogens. The greater nitrogen content found in soils beneath this type of shrub may suggest that free-living microorganisms are more active or that there are greater populations of soil organisms fixing atmospheric nitrogen.

(**a**) Roots measuring up to 10 metres in length perform hydraulic lift allowing shrubs, such as (**b**) *Piliostigma reticulatum*, to grow year-round, including through periods of drought. (RDI, BAB)

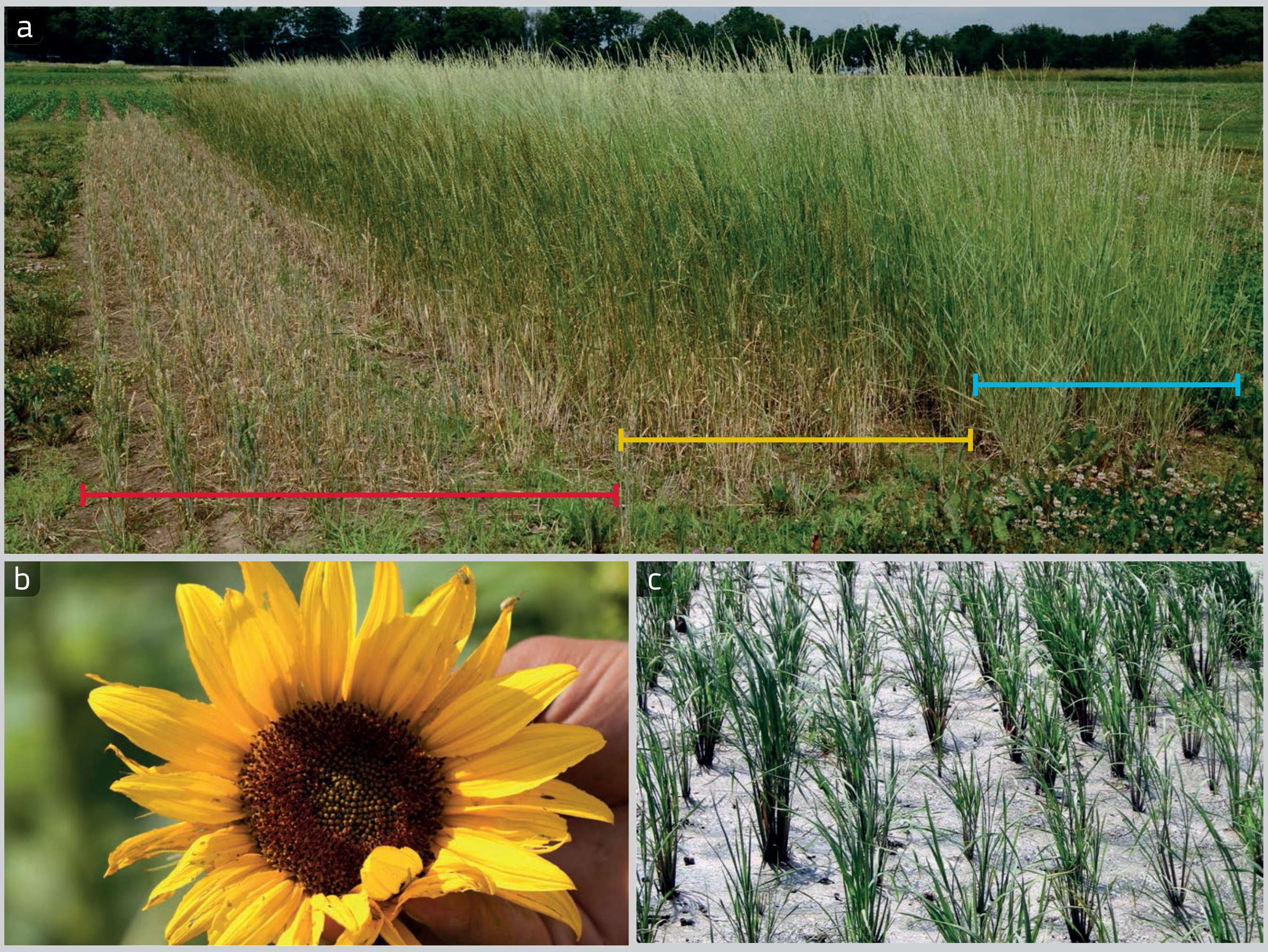
Other beneficial microorganisms in the rhizosphere could be important for promoting crop nutrient availability (e.g. phosphorus mineralisation or solubilisation – see page 105), or be direct predators of pathogens.

Furthermore, the greater carbon inputs and year-round water supply in the shrub rhizosphere could create a balanced microbial community that suppresses soil-borne pathogens (see pages 108-109) through competition.

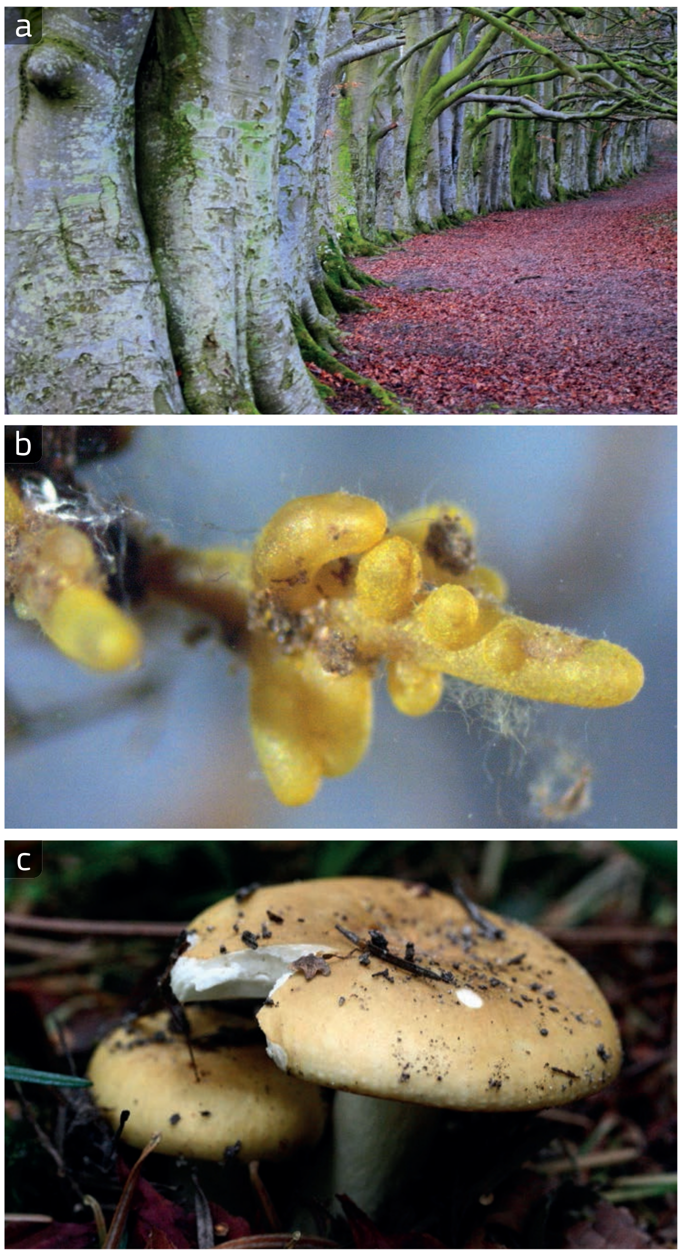
The contribution of trees to increased soil biodiversity can be attributed to their perennial nature which profoundly impacts microclimate and soil properties, including water availability, and influences the abundance, diversity and activity of soil biota required to sustain critical biological functions underpinning soil-mediated ecosystem services (see Chapter IV).

Perennial cropping systems

- Most of our food crops, such as cereal grains, legumes and oilseed crops are annual plants. An annual plant completes its lifecycle, from germination to the production of seed, within one year. There are also biennial plants that take two years to complete their life cycle. Examples of biennial plants are members of the onion family, some members of the cabbage family, fennels and carrots.
- A perennial plant lives for more than two years. Once established, perennial crops have extensive root systems with increased access to nutrients and water deep in the soil. One downside to perennial crops is that their seed yield is generally lower than that of annual crops.
- Tightening of carbon and nutrient cycling in perennial compared to annual crops results in significantly lower nitrate leaching losses, as well as increased labile soil carbon essential for sustaining soil biological activity.
- Current research efforts toward sustainable production of annual grains include rotations with perennial grain crops, such as perennial wheat (obtained through several crosses of annual wheat *Triticum aestivum* with perennial grasses, such as *Thinopyrum intermedium*) and other species related to wheat and Kernza wheatgrass (*Thynopyrum intermedium*).
- Other perennial crops are: sunflowers, rice and sorghum. They have been developed through crossing with wild species by plant geneticists.



(**a**) Field showing side-by-side rows of annual wheat (behind red line), perennial wheat (behind yellow line) and Kernza wheatgrass (behind blue line). (**b**) Perennial sunflower obtained at the University of Minnesota (USA) and (**c**) perennial rice tested in China. (SSN, CWR, DEM)



The presence of trees, for example (**a**) beech (*Fagus sylvatica*), can promote the development of specific interactions, such as (**b**) symbiosis, with soil organisms, such as (**c**) the fungus *Russula ochroleuca*. (SNA, MB, JON)

No-till farming

Global trends

The plough has always been a strong symbol of modern agriculture (see pages 122-123). However, the adoption of no-till farming has gradually increased since the 1970s as a way of dealing with problems of soil erosion and fertility. The availability of herbicides as an alternative to ploughing for weed control has played an important role. Starting in South and North America, no-till farming has spread to Australia, parts of Asia and, to a lesser extent, Europe and Africa. The area of no-till arable land is estimated at 116 million hectares globally and covers a wide range of climates, soil types and crops. [181]

No-till systems minimise mechanical soil disturbance by using direct seeders and allow for the maintenance of a permanent soil cover in the form of crop residues or cover crops (see pages 142-143). These practices include suitable crop rotations to prevent the build-up of pests and diseases. Systems that combine these three principles are known as 'conservation agriculture'. Besides erosion control and water conservation, the reduction of production costs is an important driver of no-till adoption. On the one hand, when combined with crop residue retention and/or cover crops, no-till can have important benefits for soil life. Indeed, soil organisms are considered even more important for soil functioning and crop production in no-till soils, where they take over some of the functions otherwise initiated by mechanical ploughing, such as breaking up compacted soil, incorporation of organic matter and nutrient mineralisation (see Chapter IV).

Continent	Area (hectares)	Percentage of total
South America	49 579 000	46.8
North America	40 074 000	37.8
Australia and New Zealand	17 162 000	11.5
Asia	2 530 000	2.3
Europe	1 150 000	1.1
Africa	368 000	0.3
World total	115 863 000	100

Area under no-till per continent (derived from Derpsch *et al.*, International Journal of Agricultural and Biological Engineering, 2010). [182]

Main steps of a no-till management system: (**a**) direct seeders sow in soil with plant residues from previous season; (**b**) young maize plants grow on maize residues; (**c**) plant residues in a maize field after harvesting remain until the following season, when direct seeding takes place. (USB, JJO/NRCS)

Effects on soil biodiversity

Tillage can have detrimental effects on soil life. However, some organisms are more affected than others, depending on feeding strategies, habitat preferences and reproductive capacity. Harmful impacts can be direct (e.g. body damage or increased predation). In the longer term, the indirect effect of habitat disturbance is probably more important. Soil tillage, especially when the soil is inverted, results in the incorporation of crop residues and destroys pre-existing burrows or nest structures. This strongly affects epigeic soil organisms (those feeding on plant litter at the soil surface) and soil ecosystem engineers (e.g. earthworms – see box on page 95). A third mechanism is the change in soil moisture and temperature, with bare, ploughed soil being more prone to fluctuations and extremes. As a general pattern it has been shown that soil fauna (see Chapter II) with larger body sizes and slower reproduction/longer generation times are most sensitive to the impact of ploughing.

Many soil organisms, such as (**a**) earthworms, benefit from no-till as (**b**) during ploughing they become easy prey for birds or are killed by agricultural machinery. (HRI/NRCS, TFG)

All soil fauna impacted by ploughing will benefit from no-till management. Considering soil microorganisms, no-till increases the importance of fungi relative to bacteria (see pages 33-35) as primary decomposers (see page 96), while ploughing creates conditions favourable to bacteria that are more disturbance-adapted and have higher metabolic rates. These changes can have important consequences for the structure of the soil food web in no-till versus ploughed soils and, subsequently, for organic matter decomposition and nutrient dynamics (see pages 104-106). Furthermore, no-till systems are characterised by an accumulation of crop residues on the soil surface and concentration of soil organic matter in the upper layers of the soil. Fungi and fungal grazers (e.g. collembolans – see page 50) are comparatively more important and nutrient mineralisation is often delayed due to higher nutrient immobilisation (high C:N ratio – see page 106). This can also impact plant growth as it changes the synchrony between nutrient availability and crop needs and can result in crop nutrient deficiencies or, on the positive side, reduce nutrient emissions from the system. In practice, the outcome in terms of nutrient-use efficiency by plants will depend on the interactions between crop type, activities of soil organisms, organic matter quality, soil type and climatic conditions. Changes in nutrient dynamics should therefore be accounted for when optimising management of a no-till system in order to ensure successful plant growth.

No-till, earthworms and termites

Earthworms and termites are called soil ecosystem engineers (see box on page 95). Their feeding, burrowing and nest-building activities strongly affect the soil structure and they can incorporate large amounts of organic matter into the mineral soil. By modifying the habitat of other organisms, they indirectly affect flows of energy, nutrients and water. Their impact on physical soil conditions can be impressive (see pages 110-113). Earthworms (see page 58) contribute to stable soil aggregation, and both earthworms and termites can break soil crusting and greatly improve rainfall infiltration.

Soil ecosystem engineers can, therefore, play a key role in (agro)ecosystem functioning. It has been found that no-till systems generally support larger and/or more diverse earthworm communities. A shift in relative abundance of different ecotypes is also observed. Epigeic and anecic species that feed at the soil surface especially benefit from no-till, whereas endogeic species that live and feed inside the mineral soil do well in ploughed systems in which crop residues are incorporated. Less is known about the impact of tillage on termites (see page 55), although it is generally assumed that soil disturbance negatively affects species that build subterranean nests. Foraging on crop residues by termites, however, can pose a challenge to maintaining an organic soil cover in tropical no-till systems.

No-till and arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF – see page 40) are an integral component of terrestrial ecosystems that form symbioses with most plant families, including agricultural crops. In this symbiosis, plants supply carbon substrates to AMF and receive nutrients in return, such as phosphorus and nitrogen (see page 98). AMF can also increase drought tolerance and suppress diseases, while their extraradical hyphae can bind soil particles mechanically and chemically to form stable aggregates.

AMF are mostly negatively affected by soil tillage through different mechanisms that affect the propagation structure of AMF (i.e. spores), extraradical hyphae and colonised root segments. One of these mechanisms is the dilution of spore numbers as a result of soil mixing. More importantly, tillage destroys the mycelial network and reduces mycorrhizal infectivity, thereby affecting nutrient acquisition, especially during the early stages of crop growth. Tillage reduces both AMF densities and species richness.

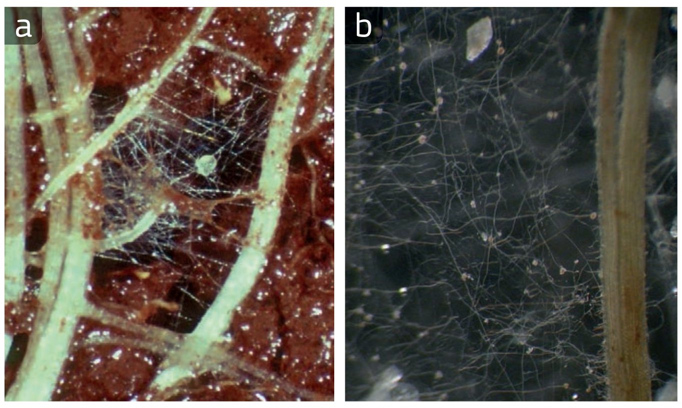
(**a**) Earthworms are the dominant ecosystem engineers in temperate areas, whereas (**b**) termites are more abundant in the arid to sub-humid tropical climates. No-tillage systems foster these two groups of soil-living organisms. (SLA, DFA)

Organic farming

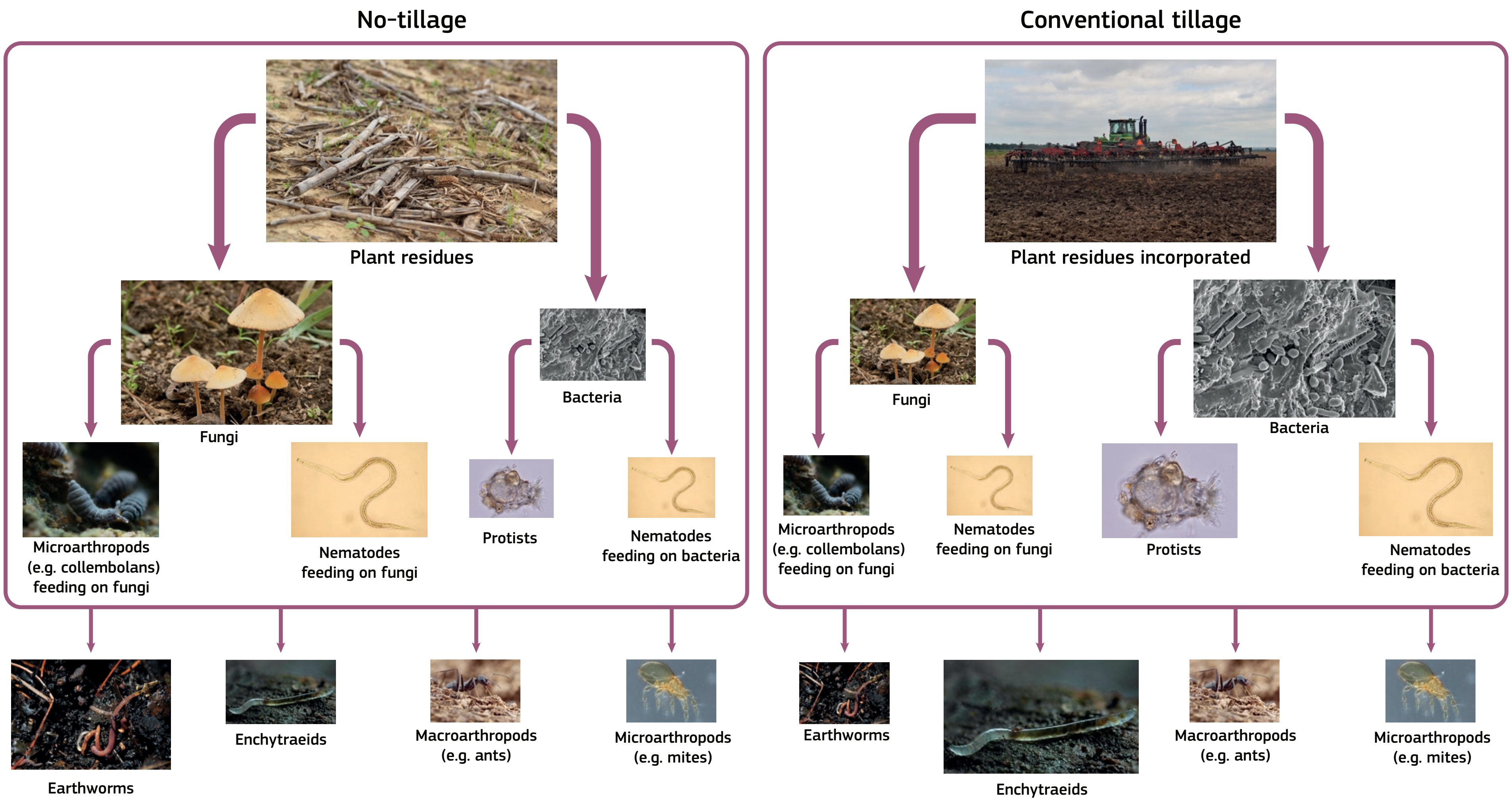
- Organic farming is a form of agriculture that relies on more natural production techniques, such as crop rotation, reduced tillage or no-till, biological pest control, and manure, green manure or compost application. It excludes, or strictly limits, the use of mineral fertilisers and pesticides.
- Organic farming relies heavily on the natural decomposition of organic matter by soil organisms, especially microorganisms (e.g. bacteria and fungi), to replace nutrients taken from the soil by previous crops.
- This biological process has been referred to as 'feeding the soil to feed the plant'.

In 2013, 78 million hectares worldwide were managed organically. (CPA)

Drastic shifts in community composition indicate that different AMF species vary in their tolerance to tillage. Indirectly, modifications in physical soil properties or soil nutrient contents in response to soil tillage, as well as changes in weed populations that act as host plants, can influence soil microbial numbers, diversity and activity, including AMF communities. However, long-term no-till farming can also result in soil surface hardening which is unfavourable for AMF distribution.



Arbuscular mycorrhizal fungi form (**a-b**) networks of fungal filaments (hyphae) that increase soil structural stability and resistance to erosion. No-till management promotes the growth of these fungi. (KR, MGU)



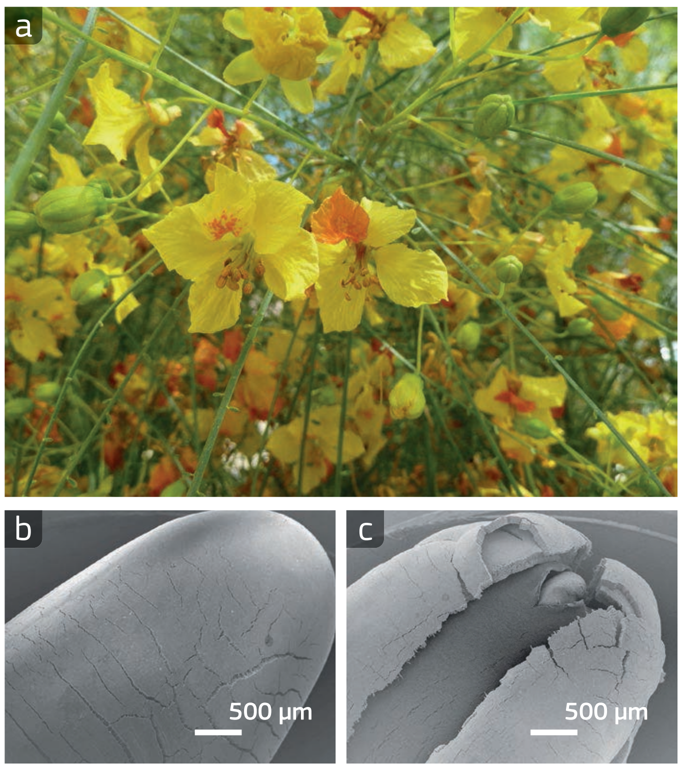
Two simplified models of food webs in no-tillage and conventional tillage agroecosystems. Larger images represent dominant soil organisms (derived from Hendrix *et al.*, BioScience, 1986). (USB, LWE, ADO, AM, SCN, EDM, CW, SSH, AZA, JRC) [181]

Fire management

Benefits of fire

Fire can threaten soil biodiversity both directly due to heat and combustion or indirectly through post-fire soil erosion and degradation. Pages 126-127 describe how fire is a natural part of nearly all terrestrial ecosystems, and that fire only threatens soil biodiversity when the balance between burning and recovery is disturbed by human activity. In this section we, will take a closer look at how fire management may promote or conserve soil biodiversity. [183]

Over time, some plants have evolved to adapt to fire. One of the best known adaptations is pyriscence, which occurs when a plant releases its seed in response to fire, in an ecosystem with relatively short fire return intervals and where post-fire conditions offer improved seed germination and seedling survival. In addition to the physical opening of the seed pod, the heat from the fire can also stimulate or inhibit the germination of seeds in the soil. For example, thermal cracking of the seed coat of jelly bean tree seeds has been observed after being exposed to 200 °C for one minute and eight minutes. The resulting fracture pattern after one minute is thought to be indicative of having overcome seed coat-enforced dormancy. The deeper fracturing after eight minutes heating exposes internal parts of the seed, thereby killing it. Research has also revealed that the smoke from a fire can promote seed germination, without any thermal effect. Smoke has been observed to produce a chemical scarification on the seed surface and an increase in the permeability of the internal cuticle, both of which significantly increase the rate of germination.



Scanning electron micrographs of thermal cracking of (**a**) jelly bean tree (*Parkinsonia aculeata*) seeds: (**b**) at 200 °C for 1 minute and (**c**) at 200 °C for 8 minutes (WCU, KSO).

Effects on soil biodiversity

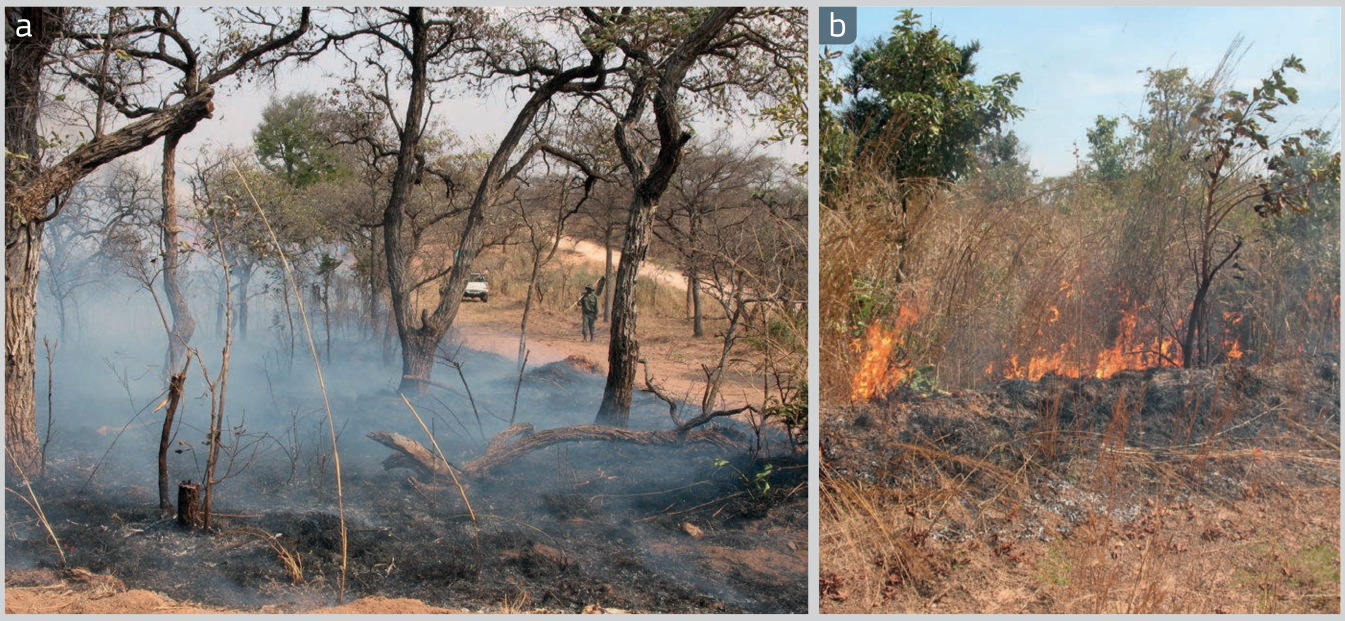
Our understanding of the beneficial interactions between fire and belowground biodiversity is very limited. An increase in soil microbial activity is often seen shortly after a fire when more substrate or nutrients are available. After varying time periods, the microbial activity is generally observed to return to pre-fire levels, or lower. Changes in soil microbial community structure (e.g. species abundance) have also been observed. However, observed patterns are highly variable and there are insufficient data to obtain a clear understanding of the relationship between fire and aspects of soil biodiversity (e.g. abundance, species richness and functional diversity).

As a form of disturbance, fire may be expected to increase species richness at a moderate intensity or frequency, as suggested by the 'intermediate disturbance hypothesis'. This states that the highest diversity of species in an ecosystem is maintained by a level of disturbance half way between frequent and rare disturbance. Therefore, in principle, an appropriate use of fire might preserve high levels of diversity. However, what this fire intensity or frequency, or combination of the two, would be for all aspects of soil biodiversity across the range of terrestrial ecosystems, remains largely unknown and requires further research. Therefore, the application of controlled fires to promote soil biodiversity still remains largely unexplored.

Wildfire causes the seed pods of the (**a**) needle bush (*Hakea sericea* Schrader) to (**b**) open, thereby (**c**) releasing the seeds. Some plant species benefit from fire to release their seeds and start their next generation. (JTA, BSC)

The 'Fire Continent'

- Africa is known as the 'Fire Continent' because prescribed burning is a widely recognised and essential ecological factor for managing its savannah ecosystems (see page 82).
- Research investigating fire regime effects on biodiversity has led to a general understanding of the effects of the type and intensity of fires, and the frequency of burning on vegetation.
- The use of fire as a range management practice (known as burning system) has been shown to be beneficial, and viable prescribed burning programmes have been developed for the grassland and savannah areas used for both livestock production and wildlife management.
- Prescribed burning has proven to be very cost-effective and has significantly reduced the hazard of large-scale wildfires.



Controlled fires in (**a**) South Africa and (**b**) Benin. Burning systems support the control of wildfires in African parks. (IPA)

Soil erosion control

Practices for erosion control

Soil erosion control measures are well established and understood but, surprisingly, still not broadly implemented. There are still many farmers around the world that have not put in place erosion controls and continue to lose tonnes of soil every year. The main reasons for this lack of implementation is that most forms of erosion control require an initial economic investment for a longer-term benefit, they can take up some of the land that otherwise could be cultivated and profitable, and more labour is needed. Therefore, a long-term vision of soil maintenance is required and, even if the vision is there, factors such as lack of land tenure (i.e. the relationship, whether legally or customarily defined, among people, as individuals or groups, with respect to land), determines whether erosion control measures will be effectively implemented or not. [184]

Practices that mostly control erosion by shortening the run or flow paths are the installation of windbreaks, terracing and ploughing and cultivating along the contour lines. The establishment of grass strips within and on the borders of fields also shortens the paths. They are mostly installed in sections of the field most prone to erosion in order to hold the soil in these vulnerable places by grass roots. Similarly, trees hold soil in place with their roots (see pages 144-145) and produce litter that can be used as a mulch.

Effects of erosion control on soil

As a result of the above-described erosion control practices, some fundamental changes also take place in the soil that actually further prevent soil erosion.

Practices to reduce soil erosion: (**a**) inclusion of trees in agricultural fields helps to hold the soil in place, thereby reducing erosion; (**b**) terraced fields decrease both erosion and surface runoff; (**c**) planting of trees around fields as windbreaks is an effective approach to reducing wind erosion; (**d**) establishing a mulch cover on the soil surface reduces the impact of rainfall on the soil, thereby reducing erosion. (JSI, ADW, ECO/NRCS)

In general, any soil-erosion control practice will 1) reduce how much the soil is exposed to running water or wind and 2) hold the soil as much as possible in place. Therefore, the practice reduces soil disturbance, covers the soil, reduces the length of the water-running or wind-flow path and increases the root biomass holding the soil. For example, no-tillage practices have been adopted for erosion control because they strongly reduce the disturbance of the soil, and the resulting residue layer on top of the soil increases the cover (see pages 146-147). In some agricultural systems, tillage is reduced rather than completely stopped, and plant materials are added to the soil surface for mulching.

The main method used to increase soil cover is by planting cover crops over the winter in order to avoid bare soil being exposed to the harsh winter elements (see page 143). Once the winter is over, the farmer needs to prepare the soil, plant and fertilise; in recent decades this has been done with heavier and heavier equipment leading to soil compaction. However, now there is a tendency to make the machinery and tyre pressures lighter.

The most significant change is that the soil structure improves because of increased root biomass (see page 43), less physical disturbance, and increased soil biotic activity (e.g. earthworms and fungi – see box to the right); all of these improvements increase soil organic matter as a binding agent that holds together soil particles in greater soil structures.

The soil biota plays an especially crucial role in cementing particles together into stable structures. For example, the burrowing of earthworms through the soil leads to the formation of pores against aggregates and burrowing walls. The fungi entangle, just like roots, particles together, and they also produce sticky organic materials that bind particles.

The improved soil structure leads to greater soil stability that can better withstand the impact of rainfall, water runoff and wind. It also increases water infiltration into the soil, thereby reducing water running off the soil surface, which causes erosion.

Effects of erosion control on soil biodiversity

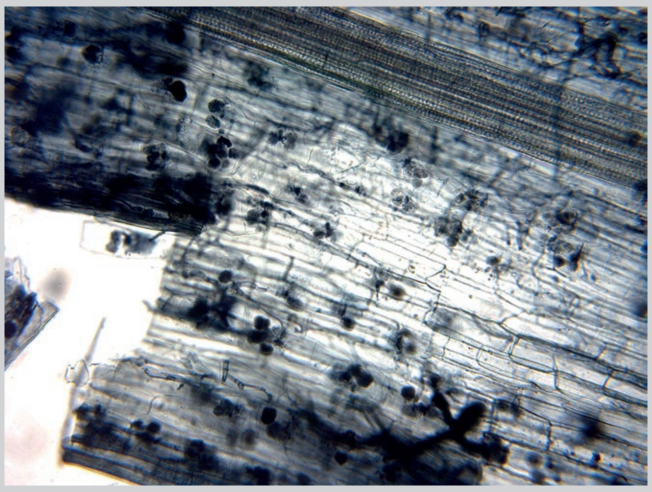
The most direct way that erosion control affects soil biota is by reducing the disturbance of the soil (see pages 128-129). For example, it is well known that no-till systems allow earthworms and fungi to thrive because they are no longer physically cut up by the plough.

Soil erosion control allows for an increase of earthworm burrowing activity. This helps create pores that further reduce water erosion effects. (LBE/NRCS)

In more general terms, any erosion control practice that leads to an improved soil structure will enhance the habitats for soil biota by forming a soil structure with numerous pores and aggregates (see page 72). A good pore structure will lead to a balance between oxygen, water and food for soil biota that need oxygen to survive. In contrast to the pores, the inside of the aggregates contain less oxygen, which is ideal for other biota. An improved soil structure can also better protect the soil biota against pollutants, drought and extreme dry-wet cycles (see Chapter V). Therefore, soil erosion controls indirectly protect many habitats in which different soil biota can survive.

Arbuscular mycorrhizal fungi vs. wind

- Arbuscular mycorrhizal fungi (AMF – see page 40) form symbiotic associations with the roots of most plant species and can improve both plant growth and soil structure. [185]
- AMF improve soil structure and stability with their vast underground network of fungal filaments (hyphae).
- Laboratory wind tunnel experiments were carried out to assess whether AMF were able to increase soil resistance to wind erosion.
- Researchers demonstrated that arbuscular mycorrhizal fungi have the potential to increase the protective effect of newly seeded plants against wind erosion.



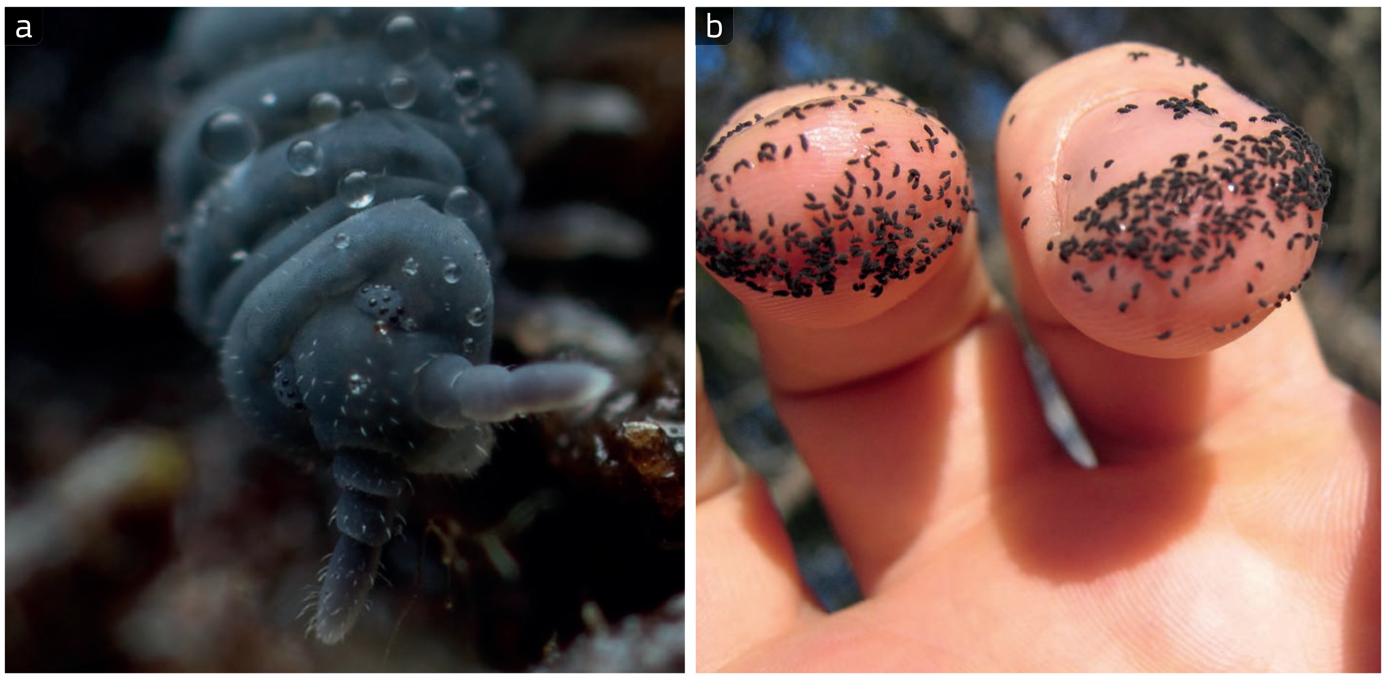
A section of a plant root with the arbuscules, the typical structures formed by arbuscular mycorrhizal fungi. AMF form a network of filaments outside plant roots that increase resistance to wind erosion. (MST)

Soil amendments

Organic amendment

Soil organic matter decline and land degradation are major concerns worldwide because they have negative consequences for soil fertility and belowground biodiversity (see pages 130-131). Soil biota contributes to the fertility of soils by decomposing organic detritus and recycling nutrients, and is vital in building up and maintaining soil aggregates, thereby improving soil aeration and water-holding capacity (see Chapter IV). A positive correlation between soil community biomass and soil fertility has been accepted for a long time, and there is growing evidence that maintaining soil biodiversity is essential to ensuring soil functioning. In fact, some soil processes (e.g. soil respiration) may be carried out by a vast array of species, but others (e.g. some reactions of the nitrogen cycle – see page 105) depend on very precise functional groups consisting of a few species; they can even be species-specific (e.g. nitrogen-fixing bacteria – see pages 33-34). [186]

Spring in a derelict cropland (**a**) before and (**b**) one year after fertilisation with sewage sludge in Spain. Test plots for Andean forest restoration with different doses of sewage sludge in Colombia show that plant cover is proportional to the amendment dose (**c**) six months and (**d**) two years after sludge application. (JML, JIB)



The application of organic amendments allows for the growth of the fungi and the species that feed on them, such as (**a**) collembolans, to (**b**) proliferate. (AM, DES)

Providing adequate levels of organic matter is central to restoring fertility and diversity to soils degraded by overexploitation, erosion or land degradation. Farms and cities produce huge amounts of carbon-rich wastes (e.g. sewage sludge and manure) that are suitable for this purpose.

The impact of organic amendments on soil biota depends on the application rate and frequency and on the physicochemical characteristics of the amendment (mainly carbon and nitrogen content and organic matter stability). As a general rule, organic amendment enhances soil microbial biomass and metabolic activity, with changes in microbial diversity ranging from no effect to modifications of the whole community structure, including shifts in the fungal-to-bacterial ratio.

Single application leads to long-lasting differences in organic carbon content between amended and non-amended soils and also to differences in microbial diversity that tend to disappear within a couple years. Microbial communities of non-amended and repeatedly amended soils differ in microbial structure and composition, but not necessarily in the ability to drive soil functions. Excessive fertilisation, however, may negatively impact key functional groups, as is the case for arbuscular mycorrhizal fungi (see page 40).

Soil invertebrates also benefit from organic amendments that increase the availability of food resources and suitable microhabitats. Composted wastes particularly boost total soil microarthropod abundance and biomass (see Chapter II). Global invertebrate biodiversity is rarely significantly altered by amendments, although significant changes in the trophic community structure may take place. A frequent feature is the relative increase of fungivorous (e.g. collembolans and mites – see pages 49-50) and predaceous (e.g. mites) functional groups when the organic matter added to the soil has been stabilised through the composting of green wastes. Conversely, amending soil with labile organic matter favours bacterial-feeders and opportunistic groups. Oribatid mites are very sensitive to the chemical quality of the amendment, and their abundance and diversity is negatively influenced by the decreasing abundance of fungi and by saline or polluted organic amendments. Nevertheless, applications of organic amendments on poor soils can be used in order to restore degraded ecosystems and allow soil biodiversity to proliferate.

	Soil Number of individuals	7 % sludge Number of individuals	15 % sludge Number of individuals
Isopoda	14	743	257
Pseudoscorpiones	14	0	57
Dermaptera	14	0	0
Protura	543	157	86
Diplura	1000	1657	1286
Symphyla	14	43	43
Pauropoda	457	314	943
Diplopoda	71	14	0
Chilopoda	200	471	329
Coleoptera	14	100	57
Coleopteran and dipteran larvae	685	558	1143
Collembola	6743	12900	16957
Acari	8940	9180	24572
Total	18709	26137	45730

Effects of different doses of an organic amendment on belowground microarthropod abundance. A mining area was reclaimed with soil previously stripped from the operation area (soil), and with this same soil amended with 7 % and 15 % (dry weight) sewage sludge. Soils were sampled five years after amendment (derived from Andrés *et al.*, Applied Soil Ecology, 2011). (PA) [186]

Vermicompost: worms at work

- Vermicompost is the product of the decomposition of vegetable or food waste and vermicast, using various worms, usually earthworms.
- Vermicast, also called worm manure, is the end product of the breakdown of organic matter by an earthworm. Vermicompost is an excellent and nutrient-rich organic fertiliser.
- Vermicompost is rich in microbial life and can be applied to poor soils.
- Large-scale vermicomposting is practiced in Canada, Italy, Japan, Malaysia, the Philippines and the USA.
- For vermicomposting at home, a large variety of bins are commercially available.

Earthworms producing vermicompost from food waste. (RMA)

Biochar

Biochar is the solid matter that remains after the pyrolisis (heating in low or no oxygen environment) of organic materials, such as agricultural wastes and animal manures, wastewater sludge, paper mill wastes, as well as trees or other plants. Wood charcoal, as used on barbecues, is produced through a similar process. Many people believe that biochar has beneficial value as a soil amendment and can help mitigate climate change. [187]

The idea behind biochar as a soil amendment comes from *Terra Preta*; a type of carbon rich soil found in the Amazon Basin and attributed to early pre-Columbian activities, which is highly fertile compared to the surrounding soils. Furthermore, evidence suggests that the carbon within *Terra Preta* soils has remained there for a long time, from centuries to millennia. It is thought that *Terra Preta* soils were established over extended periods of time through the addition of charcoal and other waste materials. The idea is that adding biochar to soils, as well as helping mitigate climate change, may also lead to other *Terra Preta*-like properties, such as increased fertility.

(**a**) A *Terra Preta* profile, the soil type that biochar is based on. In the Amazon Basin villagers deposited organic wastes, mixed with charcoal of their cooking fires, thus creating this fertile, black coloured soil. Grass cuttings, (**b**) before (dried grass) and (**c**) after pyrolysis (biochar). (SSC, SJE)

Biochar and soil biodiversity

Relatively little is known about the interactions between biochar and soil biodiversity. The interactions with and effects on some groups of organisms have been studied in more detail than others. For example, microbial biomass has been shown to increase in the presence of biochar. While one possible explanation of this increase is that biochar is highly porous and that this pore space can provide a home for soil microorganisms (e.g. bacteria and fungi), recent research questions this hypothesis given the limited number of microorganisms found inhabiting biochar four years after application to the soil. Interestingly, studies using stable isotopes to investigate the availability of carbon in biochar have shown that some of the biochar carbon is more readily used by microorganisms than was previously thought and, therefore, contributes toward increasing microbial biomass.

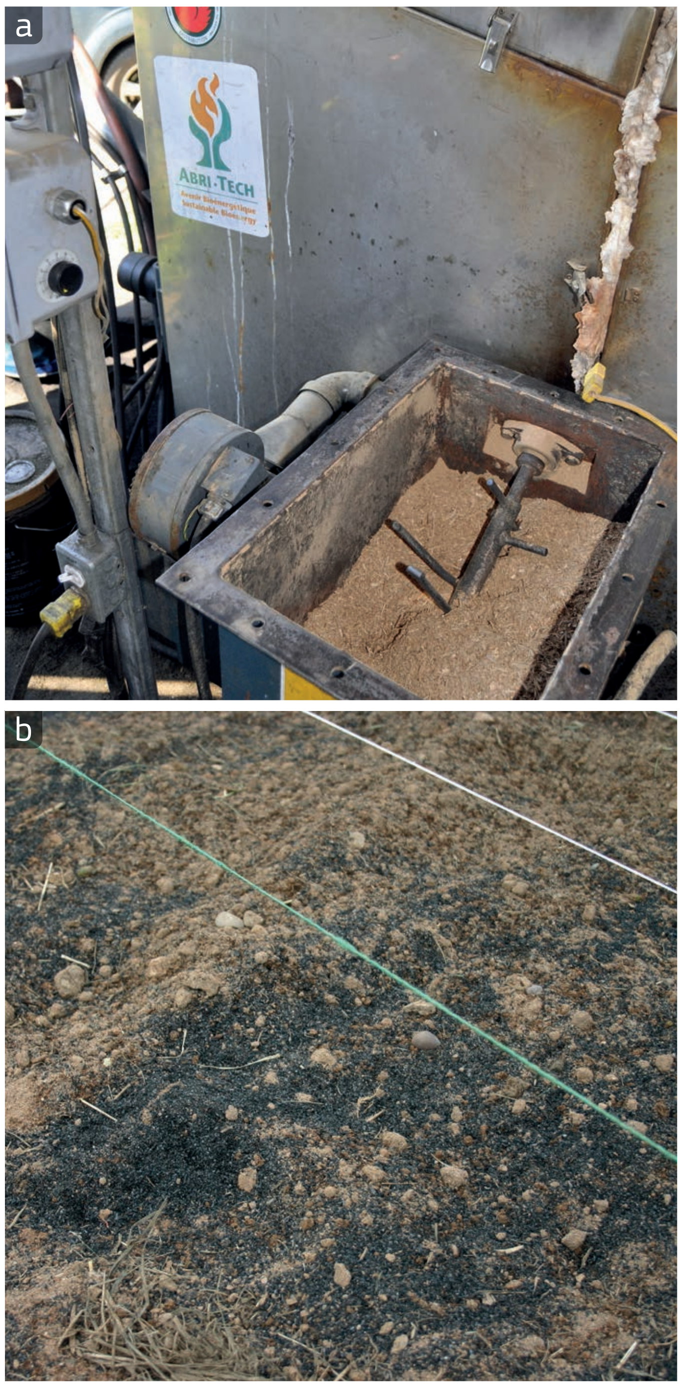
Much less is known about the interactions and effects of biochar on soil meso- and macrofauna. Earthworms (see page 58) have been shown to prefer soil and biochar mixtures compared to soil alone, although it is very likely that this is not the case with all biochars. This is because not all biochars are identical and the physical and chemical properties of a biochar are highly dependent on the original feedstock and on the conditions that were used to produce it.

Currently, there is only limited ongoing research into the effects of biochar on collembolans or mites (see pages 49-50). Furthermore, there have not yet been any studies investigating the effects of biochar on pollinators that overwinter in the soil (see box on page 61). Such pollinators provide an important ecosystem service, valued at thousand millions of dollars each year; assessing the effects of biochar application to soil on their populations remains an important but unexplored goal.

Benefits and concerns

Despite the abovementioned unknowns, biochar is regularly reported to have several positive effects, often referred to as 'wins'. These include increased soil fertility and climate change mitigation. Furthermore, biochar production also involves gases and oils that can be collected and used as biofuels. The fact that just about any carbon-rich compound can be used to make biochar has also led to suggestions that biochar production can be used to help reduce waste.

Experimental evidence suggests that biochar can indeed have beneficial properties, including increasing crop yields and reducing the emissions of other greenhouse gasses, such as nitrous oxide (N_2O – see page 103). However, whether the application of biochar to soil creates *Terra Preta*-like properties in terms of increased soil fertility in all soil types remains far from certain. For instance, contrasting effects in terms of crop yields have been reported following biochar application to soils in Europe.



(**a**) Equipment for pyrolysis produces not only biochar but also bio-oil and syngas from biomass. (**b**) Amendment of soil with biochar (black) in a garden. (MDI, CUB)

(**a-b**) Different sample sizes of biochar (MOC, ODF). (**c**) Computed X-ray tomography of biochar particles showing the fine-scale internal pore structure and high heterogeneity of a biochar sample. (SJE)

Finally, there are some concerns about the potential negative effects of biochar in some instances. Firstly, if biochar is to be used on a large scale, large areas of land will be required to grow the plants for its production, and land used to grow plants for biochar production cannot be used to grow other crops, or for nature conservation. Secondly, there is a risk of environmental contamination when biochar is applied to soil. Biochars usually contain polycyclic aromatic hydrocarbons (PAHs), which are toxic to animals and plants. However, these have been shown to remain within the biochar and not to be available for interaction with organisms. Nevertheless, this is likely to vary between different types of biochar.

Biochars can also contain other pollutants, such as heavy metals (see box on page 141), if such pollutants are in the original source material. This may be the case for biochars produced from sewage sludge.

Biochar has the potential to be beneficial in terms of soil fertility and climate change mitigation. However, it is also associated with certain risks, and its interactions with the vast array of different soil organisms are still far from well understood. Biochar research is gaining momentum, in the hope of explaining the effects and interactions when it is applied to soil in order to maximise the benefits and minimise the risks to soil biodiversity and the functions and processes driven by soil biota.

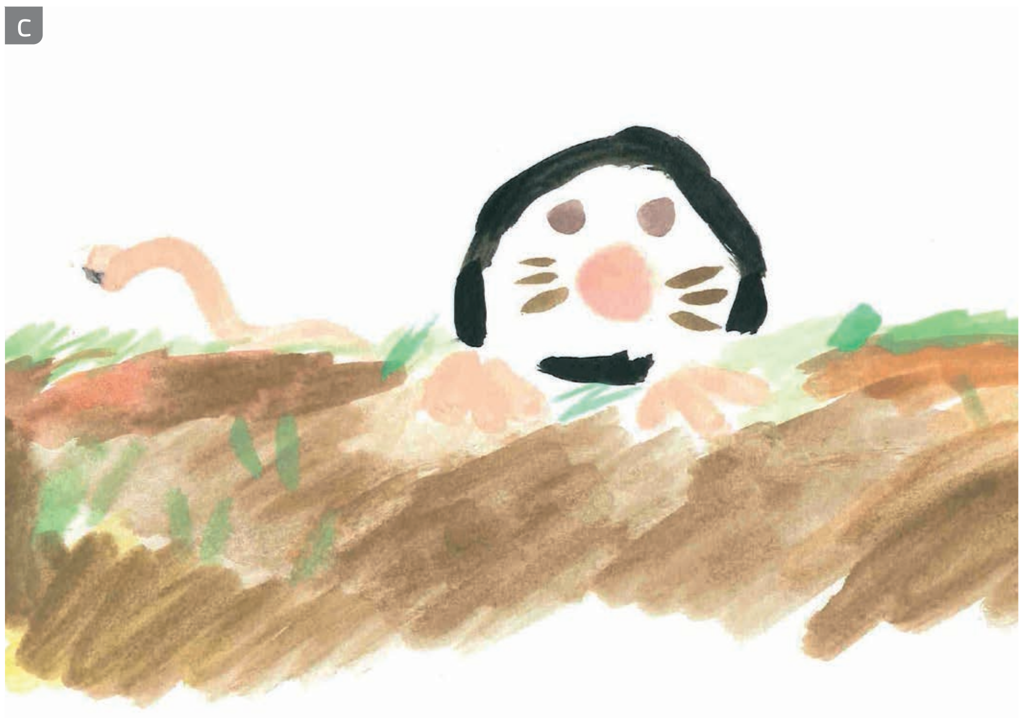
Soil biodiversity is often overlooked by policy makers and educators. However, interest in soil life dates back to a thousand years ago, and the number of studies that aim to describe the role of soil biota in a changing world is continuously increasing. There is a strong need to put soil biodiversity in the spotlight and give it the attention it deserves. (SJR, DVD, RML, MMS, TGA, KR)

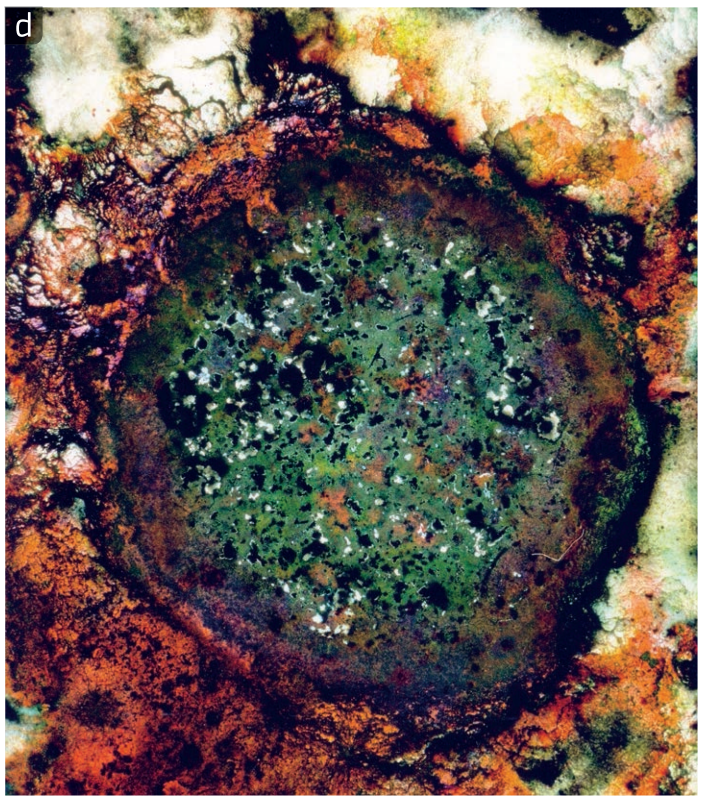
Introduction

Changes in the way human societies interact with nature to encourage more sustainable pathways also require changes in perception. Modifying the way people perceive nature is not simple. It requires a better understanding of the current status of nature, of the benefits provided to society and of ways to sustainably manage and conserve natural capital to benefit future generations.

In this chapter, the focus is on the role of environmental policies in the protection of soil as a resource. We also look at the concept of soil as a critical component of natural capital and how knowledge can shape the perceptions of society. Such understanding can guide people in making more informed decisions, ultimately leading to the sustainable management of natural resources.

Firstly, we take a look at policies that have been developed to conserve and manage soil biodiversity. Secondly, we present an overview of historical knowledge about the living soil and its management, showing how perceptions have changed through time. This is followed by examples of research projects from around the world that aim to improve our scientific knowledge of soil biodiversity. We then examine the various ways in which knowledge acquired by land managers is currently shared through participatory approaches and experiential learning that aim to conserve and manage soil biodiversity. The chapter also highlights the important role of education. Especially effective are simplified approaches, particularly for children, that help change negative perceptions about soil organisms, often resulting from an increasingly urban culture that limits both a direct interaction with nature and a balanced perception of reality. Finally, we conclude with a number of resources available to help different sectors of society become aware of the wealth of life belowground and its fundamental role in our lives on Earth.





(**a**) Knowledge sharing, (**b**) education, (**c**) awareness, (**d**) art, (**e**) historical knowledge and policy are fundamental aspects to consider in order to make society aware of the value of soil biodiversity. (NP/CIAT, KR, JRC, DMO, GPC)

Policies for soil biodiversity

Biodiversity and policy

Society in general, and policy makers in particular, have neglected soil biodiversity. Initially, no attention was given to the large biodiversity pool stored belowground and only at a later stage, during the implementation of the Convention for Biological Diversity (CBD), was attention given to this important aspect of global biodiversity.

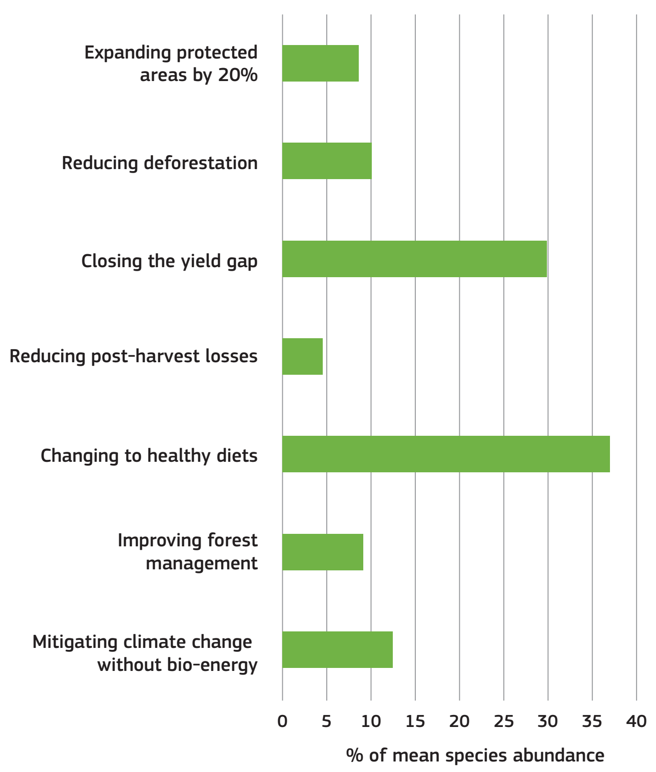
Logo of the United Nations Decade on Biodiversity. (CBD)

At its 6th meeting in Nairobi, April 2002, the Conference of the Parties (COP) of the CBD decided (COP decision VI/5, paragraph 13) '...to establish an International Initiative for the Conservation and Sustainable Use of Soil Biodiversity as a cross-cutting initiative within the programme of work on agricultural biodiversity, and invite(s) the Food and Agriculture Organization (FAO) of the United Nations, and other relevant organisations, to facilitate and coordinate this initiative'. Following that decision, an International Technical Workshop on the Biological Management of Soil Systems for Sustainable Agriculture was organised by the Brazilian Agricultural Research Corporation (EMBRAPA) and the FAO in Brazil in June 2002, to provide further elements for a coherent global approach to protecting the biological diversity of soils.

Logo of the United Nations International Year of Biodiversity 2010. (CBD)

Progress made by the FAO in coordinating this initiative was reviewed at the 8th CBD COP in Curitiba, Brazil, in March 2006. The conference adopted a framework of action for the International Initiative for the Conservation and Sustainable Use of Soil Biodiversity. This framework was intended to facilitate the implementation at national, regional and global scales of the proposed main activities and actions. Unfortunately, only a few national governments and international organisations adopted the initiative and developed national or international soil biodiversity activities.

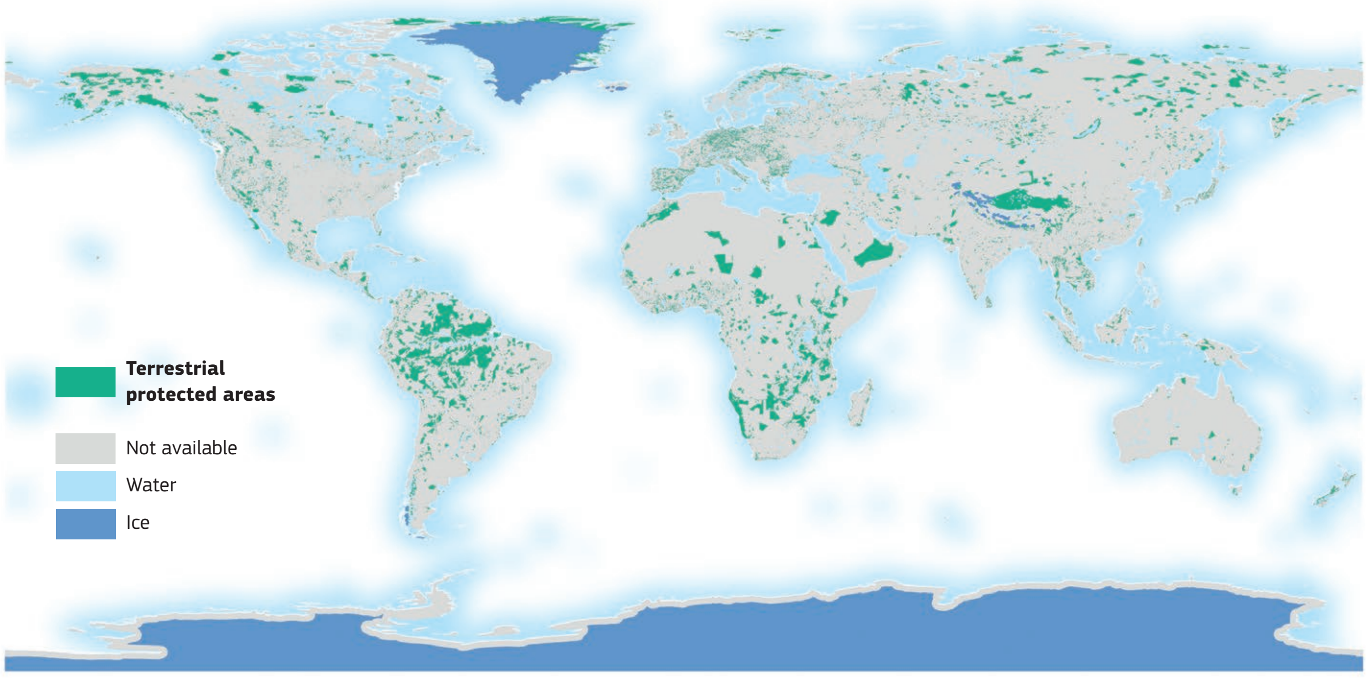
Avoided loss of mean species abundance



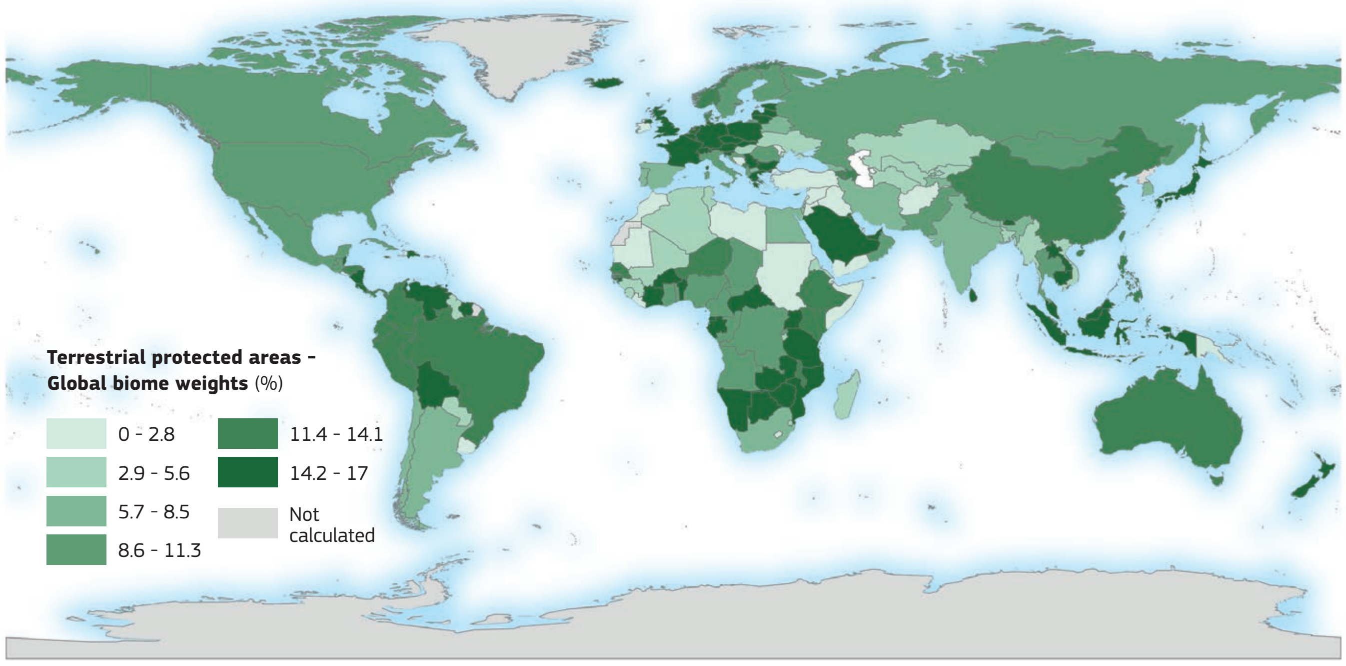
Different scenario studies and assessments have considered biodiversity loss. At the same time, options to reduce this risk have been presented. For example, 'changing to healthy diets' has most impact on reducing loss of biodiversity as it implies a rethinking of the land use. All these actions are applicable following specific policies aimed at protecting biodiversity. Unfortunately, soil biodiversity is often not considered in this type of evaluation. In the future, assessments that take soil life into account will be desirable and necessary in order to preserve soil organisms (derived from Ten Brink *et al.*, 2010). [188]

Convention on Biological Diversity

- The Convention on Biological Diversity (CBD) is a multilateral treaty brokered by the United Nations. The Convention has three main goals:
  - conservation of biological diversity (or biodiversity);
  - sustainable use of its components;
  - fair and equitable sharing of benefits arising from genetic resources.
- The Convention was opened for signature at the Earth Summit in Rio de Janeiro (Brazil) on 5 June 1992 and entered into force on 29 December 1993.
- One hundred and ninety-five states and the European Union are parties to the convention. All United Nations Member States, with the exception of the United States of America, have ratified the treaty.
- At the 10th Conference of the Parties (COP) to the Convention on Biological Diversity in October 2010 in Nagoya (Japan), the Strategic Plan for Biodiversity 2011-2020 was adopted as the basis for halting and eventually reversing the loss of biodiversity on Earth.
- The Strategic Plan for Biodiversity 2011-2020 includes five strategic goals and 20 ambitious, yet achievable, targets to be reached by 2020. These are known as the Aichi Biodiversity Targets:
  - Goal A: Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society;
  - Goal B: Reduce the direct pressures on biodiversity and promote sustainable use;
  - Goal C: Improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity;
  - Goal D: Enhance the benefits to all from biodiversity and ecosystem services;
  - Goal E: Enhance implementation through participatory planning, knowledge management and capacity building.
- In 2010, governments agreed to the Strategic Plan for Biodiversity 2011-2020 and the Aichi Targets.
- On 22 December 2010, the United Nations declared 2011 to 2020 as the UN Decade on Biodiversity.
- The United Nations proclaimed May 22nd the International Day for Biological Diversity, and 2010 the International Year of Biodiversity.



2014 map of United Nations List of Terrestrial Protected Areas. The List gives an indication of the political commitment that countries have shown toward conservation. Also, it helps to track progress towards reaching the quantitative aspect of Aichi Biodiversity Target 11: how close we are to reaching 17 % coverage of terrestrial areas and inland waters. While not explicit, it would be expected that soil organisms would also benefit from general conservation measures (derived from: IUCN and UNEP-WCMC, 2015. The World Database on Protected Areas – WDPA). (LJ, JRC) [173]



The map shows an indicator of terrestrial protected areas that measures the percentage of terrestrial habitat under protection. In particular, the map takes into account the global contribution of a country's biome protection. The global weight measures the percentage that a particular biome within a country comprises at the global level. The degree to which a country protects a biome that is rare outside its borders may matter more than protecting a biome that is plentiful elsewhere. Fifteen biomes are considered: 1) Tropical & Subtropical Moist Broadleaf Forest, 2) Tropical and Subtropical Dry Broadleaf Forest, 3) Tropical and Subtropical Coniferous Forest, 4) Temperate Broadleaf and Mixed Forest, 5) Temperate Conifer Forest, 6) Boreal Forest and Taiga, 7) Mediterranean Forest, Woodland and Scrub, 8) Tropical and Subtropical Grassland, Savannah and Shrubland, 9) Temperate Grassland, Savannah and Shrubland, 10) Flooded Grassland and Savannah, 11) Montane Grassland and Shrubland, 12) Tundra, 13) Desert and Xeric Shrubland, 14) Mangrove and 15) Snow and Ice. The indicator calculation stems from the targets set by the CBD, which establish a conservation goal of 17 % of terrestrial and inland water areas by 2020. This indicator was calculated by a joint project between the Yale Center for Environmental Law and Policy (YCELP) and the Center for International Earth Science Information Network (CIESIN) at Columbia University (USA) (derived from: IUCN and UNEP-WCMC, 2013. The World Database on Protected Areas – WDPA). (LJ, JRC) [173]

Policies for protecting soil biodiversity

While the main international agreement to protect biodiversity is the Convention on Biological Diversity (CBD), it is the responsibility of national governments to develop national policies and strategies for measuring, conserving, protecting and restoring their biodiversity resources. At the heart of these measures is legislation that prohibits the taking of species that are endangered (threatened with extinction throughout all or a significant portion of their ranges) or threatened (likely to become endangered throughout all or a significant portion of their range) within the foreseeable future. An additional protection route is to limit habitat alterations that could affect an organism (for example, destroying breeding grounds). Many people may be aware of specific acts to protect aboveground biodiversity (e.g. nature reserves, Red List, ivory export ban, greenbelts, etc.). However, it may be surprising to learn that there is virtually no explicit protection of the organisms that live in the soil.

Part of the problem is that biodiversity is a significantly complex scientific concept compared to other environmental issues, such as air or water quality. Soil biodiversity cannot be measured by simple universal indicators, such as temperature or the concentration of a pollutant. It is clear that soil biota can be offered some security where countries or regions have strong soil protection or nature conservation policies or strategies. Most soil-related legislation aims to secure or restore soil functions by limiting negative effects, such as the physical loss of soil (i.e. by reducing erosion by wind or water, land use change and the sealing of soil by urban development) or by controlling the introduction of potential toxins, such as endocrine disrupters or pesticides.

To be effective, legislation affecting soil biodiversity must be viewed within a broader context of land use planning which must reflect the multiple demands on soil but at the same time ensure that these uses are undertaken in a rational manner under the umbrella of sustainable development. However, it is worth noting that legislation by itself may not solve all issues connected with the conservation of soil biodiversity. Laws and regulations should be complemented by education, training and heightened awareness of the value of life in the soil.

Global Soil Partnership

In 2011, the Food and Agriculture Organization (FAO) took the initiative to propose a new Global Soil Partnership (GSP) as a voluntary platform that would allow for the implementation of sustainable soil management practices. More than 30 years after the adoption of the World Soil Charter, all FAO members, as well as relevant stakeholders from the private sector, NGOs and academia, joined in a common voluntary effort to take action against the rapidly increasing degradation and depletion of our limited soil resources [190]. After the establishment of the GSP, five plans of action were developed:

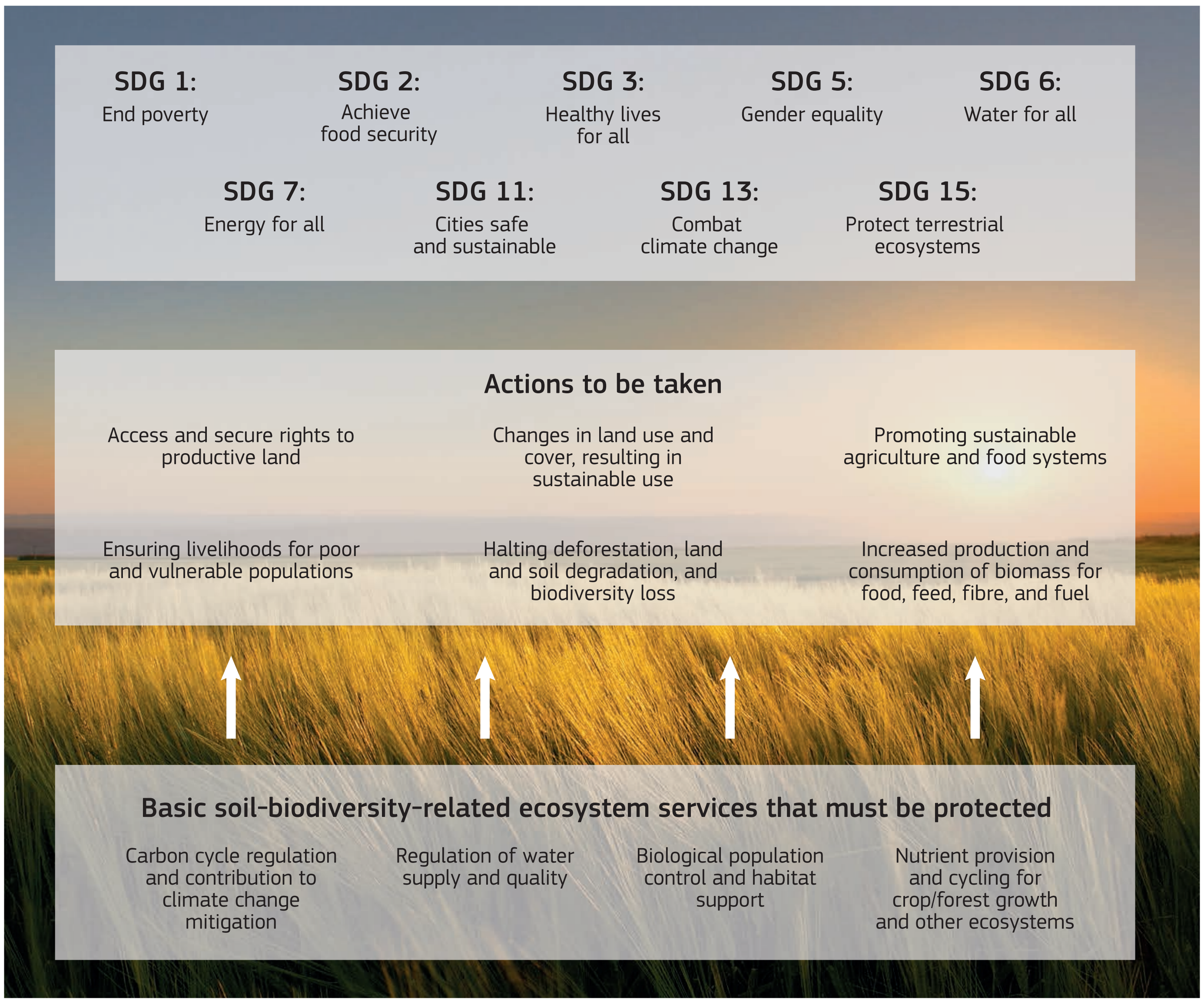
1. promote the sustainable management of soil resources for soil protection, conservation and sustainable productivity
2. encourage investments, technical cooperation, policy, education, awareness and extension
3. promote targeted soil research and development, focusing on identified gaps, priorities and synergies with related productive, environmental and social development actions
4. enhance the quantity and quality of soil data and information: data collection (generation), analysis, validation, reporting, and monitoring and integration with other disciplines
5. harmonise methods, measurements and indicators for the sustainable management and protection of soil resources

Of crucial importance to the development of these plans of action was the establishment, in 2013, of a functioning science-policy interface within the GSP: the Intergovernmental Technical Panel on Soils (ITPS). The ITPS is composed of 27 high-level soil experts representing the seven FAO regions of the world (Europe, Asia, Pacific, Africa, Near East and North Africa, South America and Mexico, and Central America and The Caribbean). Similar to the Intergovernmental Panel on Climate Change (IPCC) and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), it provides high-level policy advice on soil-related technical and scientific issues. For soil biodiversity, it has developed a close cooperation with the Global Soil Biodiversity Initiative and the IPBES in order to assure a full assessment of global soil biodiversity and the necessary information for implementing adequate policies to protect this important biodiversity pool.

2015, the International Year of Soils

- The 68th United Nations General Assembly declared 2015 the International Year of Soils (IYS).
- The Food and Agriculture Organization (FAO) was nominated to implement the IYS 2015, in collaboration with governments and the secretariat of the United Nations Convention to Combat Desertification (UNCCD).
- The IYS 2015 aimed to increase awareness and understanding of the importance of soil, including its biodiversity, for food security and essential ecosystem functions.
- The specific objectives of the IYS 2015 were to:
  - raise full awareness among civil society and decision makers about the profound importance of soil for human life;
  - educate the public about the crucial role soil plays in food security, climate change adaptation and mitigation, essential ecosystem services, poverty alleviation and sustainable development;
  - support effective policies and actions for the sustainable management and protection of soil resources;
  - promote investment in sustainable soil management activities to develop and maintain healthy soils for different land users and population groups;
  - strengthen initiatives in connection with the SDGs (Sustainable Development Goals) process and post-2015 agenda;
  - advocate for rapid capacity enhancement for soil information collection and monitoring at all levels (global, regional and national).
- In 2002, The International Union of Soil Sciences (IUSS) made a resolution proposing the 5th of December as World Soil Day to celebrate the importance of soil. In 2013, the 5th of December was declared World Soil Day.

FAO headquarters in Rome promoting the International Year of Soils. (AO)



Soil biodiversity plays a fundamental and cross-cutting role in achieving some of the Sustainable Development Goals (SDGs). In order to reach these objectives, political measures must be taken (derived from Institute for Advanced Sustainability Studies, 2015). (CRE, JRC) [189]

Sustainable Development Goals

Following the Rio+20 Conference in 2012, a process was initiated to define the post-2015 global agenda leading to sustainable development. A series of Sustainable Development Goals (SDGs) have been defined that, if implemented, could allow all of us to live on this planet in a sustainable way. The goals have a timeframe of 15 years, starting in 2015, and include a series of goals relevant to soil resources and, more specifically, to soil biodiversity.

Soils are well recognised as one of the major elements of sustainable development. Being a limited, non-renewable, natural resource, they must be managed in a sustainable way for future generations. Soils are relevant to food security (SDG 2 'End hunger, achieve food security and improved nutrition and promote sustainable agriculture'), food safety and human health (SDG 3 'Ensure healthy lives and promote well-being for all at all ages') and nature protection (SDG 15 'Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, halt and reverse land degradation and halt biodiversity loss'). Each of the SDGs includes detailed targets to be achieved by 2030.

Soil biodiversity is a key element of the proposed sustainability agenda, especially within SDG 15 which addresses terrestrial ecosystems and land degradation. Very important will be the definition of clear indicators that will allow us to measure progress towards those ambitious goals and targets. Certainly an indicator on soil biodiversity would be very helpful, not only for assessing progress towards protection and restoration of terrestrial ecosystems, but also linked to other related goals of food security and food safety.

Historical knowledge

Nature is essential for humankind

Humans have always depended on nature for their food and shelter. Early humans, by necessity making a living as hunters and gatherers, learned to read the landscape and (by trial and error) discovered which food and water sources could be found above- as well as belowground. Soil-based resources entail plant roots, mushrooms, grubs, seeds, nuts, soil-dwelling mammals, reptiles and insects. In industrialised countries, such knowledge of nature as a natural provider of food, building tools and medicine is no longer present among the majority of people.

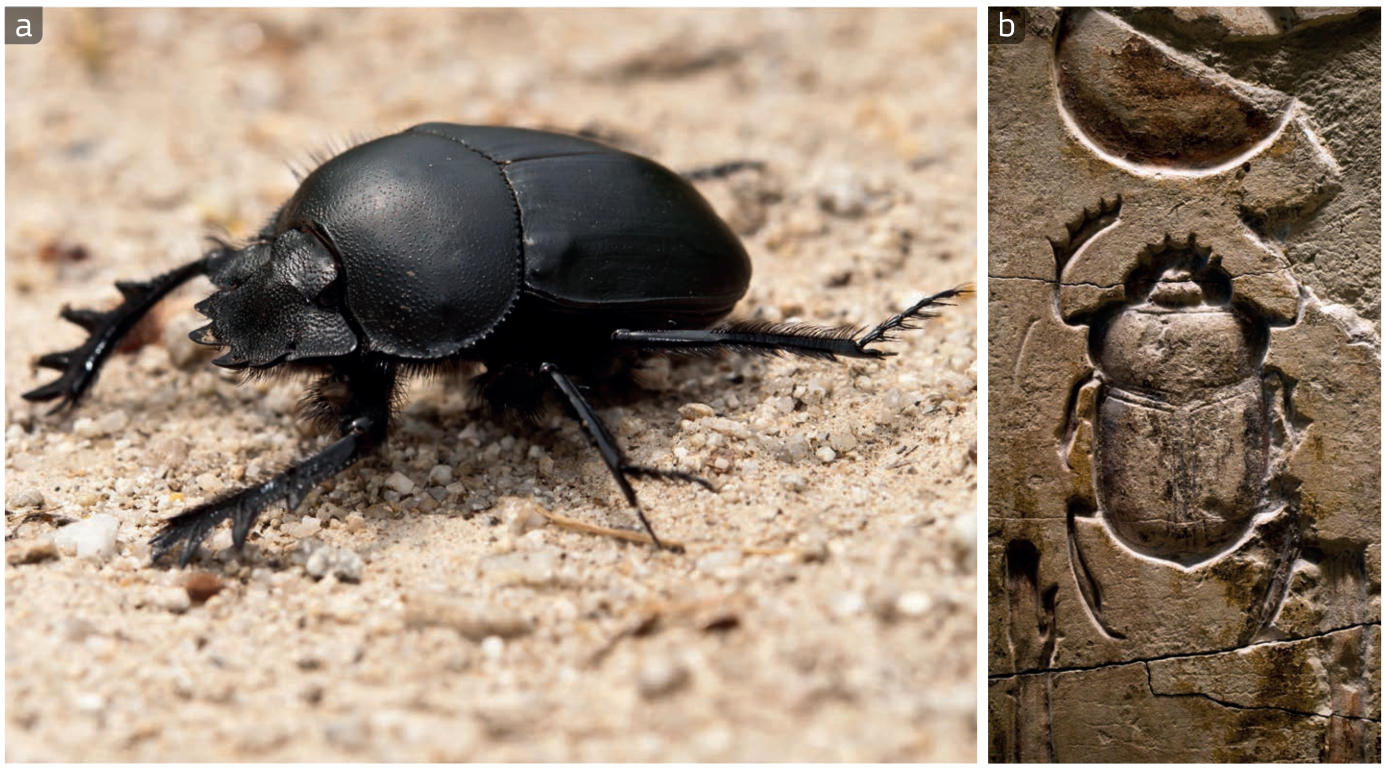
In the few ancient cultures that still exist today (i.e. the aboriginals in Australia or Bushmen in Africa), we can still find understanding of above- and belowground biodiversity and its uses; knowledge that was passed on for many generations over thousands of years. This skill was established through storytelling, songs and paintings. It is important to realise that belowground resources are not only very important as food but also for the provisioning of scarcely available water which, for example, Bushmen can obtain from plant roots.

Naro Bushman drinking water from plant roots in Botswana show the unavoidable bond between humankind and nature. (DVL)

Agriculture, soil fertility and biodiversity

Ever since the onset of agriculture approximately 10 000 years ago, mankind has modified the land and the soil. In order to clear natural land to make space for desired plant species (i.e. early crops not resembling those we know today), land was burnt. Not only did the fires create space, they also left minerals in the form of ash to the benefit of plant growth. When production declined after such slash-and-burn practices, another piece of land would be burnt and the old land left to regenerate.

This practice demonstrates knowledge of the interactions between soil properties and plants, our ability to manage it and the need for a recovery period without understanding all the specific underlying mechanisms. In fact, our understanding of the mechanisms of plant growth and the visualisation of soil organisms would only be realised in the 17th - 19th centuries. A good example of well-developed soil management is found in soils of the Neotropics. In these regions, man-made soils created 9 000 to 2 500 years ago by the activity of humans are found to be more fertile than the surrounding non-managed soil. These soils are known as Amazon Dark Earths or *Terra Preta* (see page 151).



(**a**) The dung beetle species *Scarabaeus sacer* was connected by the (**b**) ancient Egyptians with their sun god and regarded as sacred. (LKU, WTC)

Indigenous people created these soils by adding charcoal, animal bones and organic residues of plants and animals to the soil. This soil management promoted soil structure and enriched the soil with mineral nutrients, such as nitrogen, phosphorus, calcium, manganese and zinc, as well as organic matter and soil organisms. These properties have only been revealed in recent decades, but the creators and users of these soils were clearly aware of the importance of good soil management practices for increasing their crop yields.

Another classic example of the use of inherent soil biodiversity is the practice of mixed cropping of legume species, such as beans or peas, with non-legume species, such as maize or other grass species, as practiced by many ancient civilisations in China, the Middle East and Mesoamerica. This farming system makes use of biological nitrogen fixation (BNF) by legume crop roots in symbiosis with nitrogen-fixing bacteria (see pages 33-34), and benefits plant species that require a lot of nitrogen but cannot support the BNF. Legume species are good hosts for specific species of soil-dwelling nitrogen-fixing bacteria, while grass species are not because they lack the recognition system (via chemical signals) and cannot develop the root nodules that host the bacteria. The whole process of biological nitrogen fixation and the role played by specific soil bacteria was only discovered at the very end of the 19th century by the German agronomist Hermann Hellriegel and Dutch microbiologist Martinus Beijerinck.

Slashing-and-burning to prepare the land for agriculture in Finland, in 1893. (IKI)

Early descriptions of soil biota

The ecology of some soil biota achieved high worship value in ancient cultures. In ancient Egypt, the cyclic nature of days and seasons was recognised and was of central importance in mythology and daily life. In this context, the dung beetle *Scarabaeus sacer* of the family Scarabaeidae played an important role as the symbol for the sun god Ra. This god was believed to roll across the sky each day with the power to transform bodies and souls. The behaviour of the dung beetle was seen to match this cycle as the beetle rolls balls from dung and deposits its eggs inside this ball so that the larvae that hatch from the eggs have plenty of food.

The ancient Greek philosopher Aristotle wrote *Historia animalium* (History of Animals) that reports early interest in soil biology. (TEF)

The ancient Greek philosopher, Aristotle (384-322 BC), studied and wrote about many scientific disciplines, including biology. He studied plants and animals, their morphology and behaviour. Among his writings on animals, soil-dwelling insects and worms did not go unnoticed. For example, in the History of Animals he noted 'some creatures provide themselves with a dwelling, others go without one: of the former kind are the mole, the mouse, the ant, the bee; of the latter kind are many insects and quadrupeds.' [...] Further, in respect to locality of dwelling place, some creatures dwell underground, as the lizard and the snake; others live on the surface of the ground.' (translated by D'Arcy Wentworth Thompson).

'Worms are the intestines of the earth'

Aristotle, Historia animalium, 350 BC.

17th century

Given the very small size of most soil organisms, it is no surprise that it required the invention of the microscope before soil biodiversity could really be explored. The first microscopes and the descriptions of the observations of the very small organisms were initially only of academic interest. The first publication with drawings of microscopic observations was *Micrographia* by Robert Hooke, published by the Royal Society in England in 1665. The publication of *Micrographia* and its drawings greatly inspired Antonie van Leeuwenhoek (1632-1723) to further develop his own microscopes with higher resolution and to further explore microbial life.

Replica of the microscope invented by Antonie van Leeuwenhoek. Despite the limited size of his instrument, he was the first to observe and describe single-celled organisms. (NDA)

18th century

The descriptions of new species, including those of microorganisms, continued to expand in the 18th century. With respect to the discovery and descriptions of fungi, the work *Nova plantarum genera* (1729) by the Italian botanist Pier Antonio Micheli is noteworthy. Not only did it contain descriptions of 1 400 plant species that were new to science, it also comprised 900 species of fungi and lichens and recognised that the lifecycle of fungi occurs through spores (rather than from spontaneous generation).

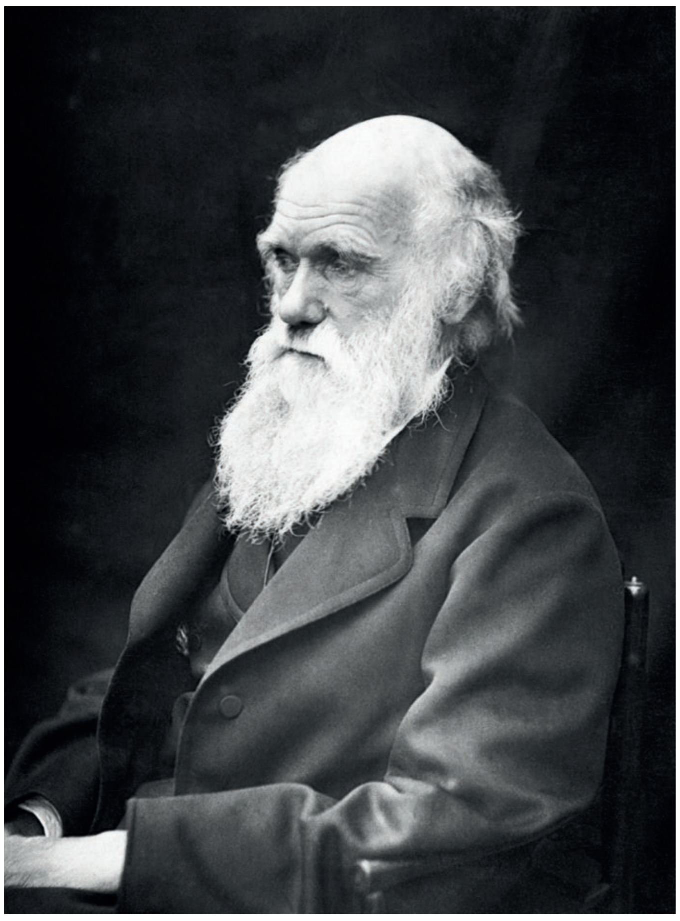
While the 18th century Swedish botanist, physician and zoologist Carl Linnaeus (see page 29) described many species of plants and animals, he also developed a simple system of naming (with genus and species names) and ordering or classifying organisms based on their (mostly morphological) characteristics and level of complexity.

In the 1st edition of *Systema Naturae* published in 1735, (**a**) Linnaeus classified the (**b**) animal kingdom (*Regnum Animale*) into six groups, with mammals ('Quadrupedia') first and worms ('Vermes') last. (MHO, ANM)

19th century

The foundations of the systematic ordering of life on Earth from unicellular organisms to humans by Linnaeus were further developed in the 19th century by the German scientist Ernst Haeckel (1834-1919) and the English scientist Charles Darwin (1809-1882). In his publication *Generelle Morphologie der Organismen* in 1866, Ernst Haeckel not only found, described and named several new species, he also related all life forms and their evolutionary development in the form of a tree (first example of an evolutionary tree). Furthermore, he is considered to be the father of ecology since the word and concept of 'Ecology' ('Ökologie') was used for the first time in that same book.

Charles Darwin is best known for his major insights into the process of the evolution of life on Earth. Less well known, but no less important, is that he can be regarded as a founding father of soil ecology. Shortly after his return from his voyage on the Beagle, Darwin showed a keen interest in earthworms and reported on an experiment with earthworms, the first ecological experiment, in The Origin of Species.

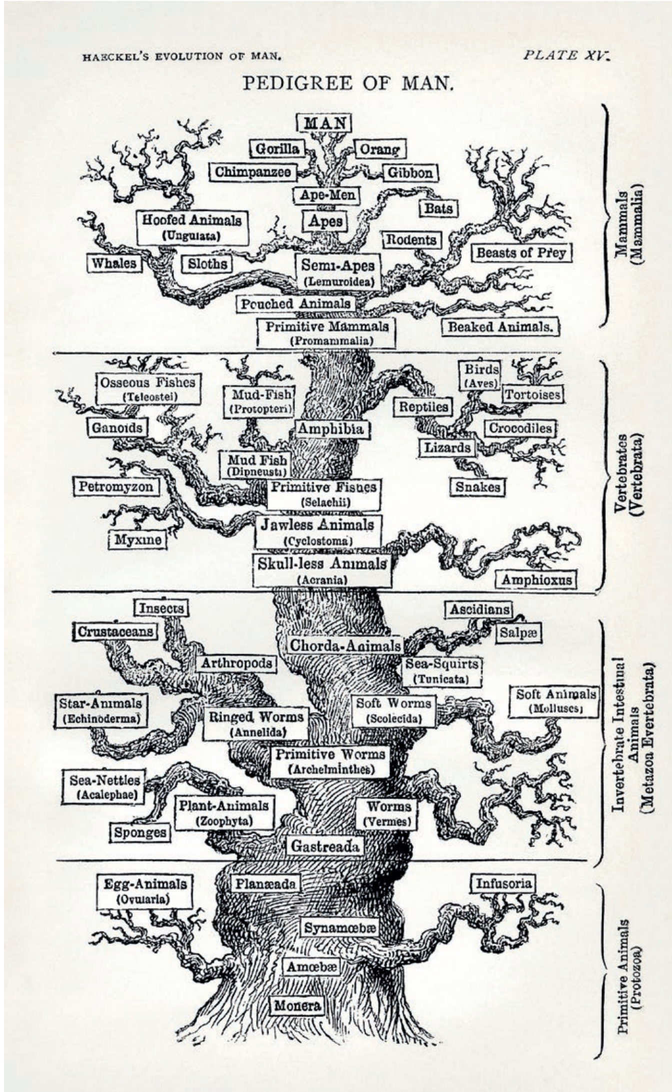


While famous for his theory of evolution, Charles Darwin (1809-1882) was passionate about earthworms. (JCA)

Darwin continued to study earthworms in laboratory experiments and field observations for 40 years, which finally resulted in the publication of his last book in 1881: 'The Formation of Vegetable Mould through the Action of Worms, with Observations of their Habits'. The response to the publication of his book was varied. It sold 6 000 copies soon after its publication. While the established scientists were initially rather sceptical about its significance, Darwin's thorough observations and experimentation on the ecology and behaviour of earthworms demonstrated that changes that seemto be small and gradual over short timespans can, over longer time periods, lead to large changes, bringing Darwin to conclude that earthworms have played a significant role in the history of the world.

Sequencing tardigrade's genome

- In 2015, scientists sequenced the entire genome of a tardigrade (see page 44). They discovered that approximately one-sixth of the tardigrade genome was 'stolen' from other species. This means that many tardigrade's genes come from other organisms through a process known as horizontal gene transfer. [191]
- The foreign DNA (see box on page 30) comes primarily from bacteria, but also from plants, fungi and archaea. Researchers think that this has allowed tardigrades to survive in extreme conditions (e.g. absence of water).
- A future challenge for soil biodiversity research will not only be the identification of all soil organisms, but also the sequencing of their genomes in order to identify new genes that, for example, might be of interest to medicine and for drug development.



Ernst Haeckel's Tree of Life, published in The Evolution of Man (1879). (EHA)

20th century

In the first half of the 20th century, the principles of animal ecology and their feeding relations were published by the English scientist Charles Elton in Animal Ecology. His ideas about the functional attributes of organisms in terms of their position in a food web were also applied belowground (see page 96). Gradually, observations and experiments clarified the ecological issues of who (which species or species groups) is feeding on/from whom. However, it was not until the 1980s that the experimental and theoretical ideas on the role of the soil food web size and composition in nutrient-cycling processes (see pages 104-105) were integrated and that the models including soil organisms' contribution started to be validated.

High-throughput DNA sequencing

- In recent years, the high demand for DNA (see box on page 30) sequencing has driven the development of high-throughput (or next-generation sequencing) technologies that accelerate the DNA reading process, producing thousands or millions of sequences concurrently.
- For example, nowadays there are instruments that provide more than 25 million sequences in only two days with 99.9 % accuracy.
- To illustrate the nature of the reductions in DNA sequencing costs and the power of high-throughput techniques, it is sufficient to consider that the cost of sequencing a genome of a human dropped from 100 million dollars in 2001 to approximately 1 000 dollars in 2015. In addition, the first sequencing of the human genome required 15 years, while in 2014 it was possible to sequence over 45 human genomes in a single day.
- Of course, these techniques can also be applied to the study of soil biodiversity to discover an unprecedented diversity of organisms living in soils.
- The future of research into soil biodiversity and, in particular, the possibility to undertake a large-scale assessment and monitoring, will be strongly influenced by the use of high-throughput technologies.

21st century

In recent years our understanding of the composition and activities of soil biota, and its evolutionary history and future potential have developed significantly due to advances in molecular biology and bioinformatics (see pages 64-65). Furthermore, this knowledge has become more accessible through dedicated websites.

Research into soil biodiversity

The Tropical Soil Biology and Fertility Programme

Several international projects remain focused on the study of soil biodiversity and its role in ecosystem functioning.

For more than thirty years since its foundation in 1984, the Tropical Soil Biology and Fertility Programme (TSBF) has promoted and facilitated research into the biological management of soil fertility throughout the tropical regions of Africa, India, Southeast Asia and Latin America. The main target of this programme has been to utilise knowledge of soil biodiversity to enhance the productivity and sustainability of agriculture practiced by resource-poor smallholder farmers, particularly those farming on degraded soils [192]. The research follows three main interlinked aims:

1. improve methods for the management of organic inputs, such as crop residues or manure, with or without mineral fertilisers
2. contribute to environmental change research by studying the impact of land-use change on the carbon cycle, particularly with respect to the role of soil organic matter in agricultural productivity
3. manipulate soil organisms and soil biodiversity for improved soil health

One of the most significant and influential outputs from this research was the development of a management tool to facilitate the choice of the most appropriate use of organic inputs for nutrient supply to crops and soil erosion control: the TSBF Organic Resource Database and Decision Support System.

All TSBF research projects have been carried out through networks involving collaboration between large numbers of national and international research institutions and universities. An essential feature of such collaboration is the use of standard methods. Two TSBF Handbooks of methods for soil research have been produced and widely used throughout the tropics. The TSBF was a pioneer in the application of participatory research on soils.

TSBF legacy

To understand the effects of different disturbances on soil biota and to compare sites and treatments, there is a need for standard methods and practical instructions for the inventory of belowground biodiversity. One of the main achievements of the TSBF is the production of texts proposing standard methods for the study of biodiversity. Handbooks for sampling soil organisms have appeared at regular intervals over the past 50 years, but more recently there has been a set of protocols focused on tropical systems, assembled and drafted by scientists affiliated with or associated to the TSBF, such as those of the Macrofauna Network, the Terrestrial Initiative in Global Environmental Research (TIGER) and the Alternatives to Slash-and-Burn project (ASB).

Methods for the analysis of some components of soil biota were included in the pioneering text in 1993 'Tropical Soil Biology and Fertility: A Handbook of Methods'. This is a manual largely devoted to physical and chemical analyses, including the study of processes, such as litter inputs and decomposition rates. However, it also recognises the importance of investigating a number of functional groups of soil organisms, including three types of earthworms and both mycorrhizal fungi and root-nodulating bacteria (see Chapter II). In 1996 another book, entitled 'Methods for the Examination of Organismal Diversity in Soils and Sediments', also developed as part of UNESCO's contribution to the DIVERSITAS Programme, presented some instructions for the analysis of soil life.

A great improvement in the standardisation of soil biodiversity investigations is proposed in the 2001 report 'Standard Methods for the Assessment of Soil Biodiversity and Land-use Practice'. This publication extends the number of functional groups of soil organisms to be considered for a reliable analysis. It adds detailed methods for the evaluation of nitrogen-fixing Leguminosae-nodulating bacteria (see pages 33-34) as well as of members of microfauna, and introduces the concept of extended (100 m) transects for sampling termites and ants.

Several publications, such as this (**a**) handbook, present (**b–d**) procedures to standardise the sampling of soil-living organisms in tropical soils. These methodologies are one of the main achievements of the Tropical Soil Biology and Fertility Programme. (FMSM, PL, GS/CIAT) [191]

The latest guide presented in the context of TSBF is the 'Handbook of Tropical Soil Biology, Sampling and Characterization of Below-Ground Biodiversity'. It was released in 2008 as an outcome of the Global Environment Facility (GEF)/United Nations Environment Programme (UNEP)-funded project 'Conservation and Sustainable Management of Below-Ground Biodiversity (CSM-BGBD)'. It further enlarges the number of functional groups of soil organisms to be analysed in a soil biodiversity survey. In more than 200 pages, sampling methods are described and identification routes recommended for ants, termites, beetles, fruit flies, earthworms, collembolans, mites, nematodes, fungi and bacteria. In addition, it includes the first extensive discussion on the issues related to soil biodiversity sampling in land-use mosaics, with practical advice on what, when and where to sample, as well as detailed schemes for land-use description and classification. Finally, a scientific paper from 2009 summarises progress towards a universal protocol for sampling soil biota in the humid tropics, including a discussion of spatial scaling and replication issues.

All these valuable publications on methods necessarily set the agenda for future belowground biodiversity projects in relation to land-use change and agricultural intensification, by specifying the groups of organisms that must be sampled or assessed. Furthermore, they raise questions on the relationships existing among species diversity, functional diversity, trait diversity, functional composition and the occurrence and intensity of ecological processes (see Chapter IV). Summarising all these aspects, one of the main achievements related to soil biodiversity of the TSBF Programme is the central role of the concept of functional group. It highlights the poor state of taxonomical knowledge for some groups of soil organisms and the lack of agreed or adequate methods to extract and enumerate others. Also, it states the need to examine all components of soil biota to obtain a reliable assessment of soil functioning and quality.

The Red List of Threatened Species

- The International Union for Conservation of Nature (IUCN) Global Species Programme working with the IUCN Species Survival Commission (SSC) has been assessing the conservation status of species on a global scale for the past 50 years in order to highlight taxa threatened with extinction, and, thereby, promote their conservation.
- Although today the political, economic, social and ecological world is very different from when the first IUCN Red Data Book was produced, the IUCN Global Species Programme, working with many partners, remains firmly committed to providing the world with the most objective, scientifically based information on the current status of globally threatened biodiversity.
- The plants, fungi and animals assessed for the IUCN Red List are the building blocks of ecosystems, and information on their conservation status and distribution provides the foundation for making informed decisions about conserving biodiversity from local to global levels. The IUCN Red List of Threatened Species provides taxonomic, conservation status and distribution information on plants, fungi and animals that have been globally evaluated using the IUCN Red List Categories and Criteria. This system is designed to determine the relative risk of extinction, and the main purpose of the IUCN Red List is to catalogue and highlight those plants and animals that are facing a higher risk of global extinction (i.e. those listed as critically endangered, endangered and vulnerable).
- The IUCN Red List also includes information on plants, fungi and animals that are categorised as 'extinct' or 'extinct in the wild'; on taxa that cannot be evaluated because of insufficient information (i.e. are data deficient); and on plants, fungi and animals that are either close to the threatened thresholds or that would be threatened were it not for an ongoing taxon-specific conservation programme (i.e. are near threatened).

Some of the endangered species of the IUCN Red List of Threatened Species are linked to soil: (**a**) the lesser mole-rat (*Spalax leucodon*), (**b**) the lichen *Cladonia perforata* and (**c**) the fungus *Pleurotus nebrodensis*. (AW, ACR, RMS)

Ecological Function and Biodiversity Indicators in European Soils

The European Union (EU) acknowledges the importance of soil biodiversity in the role of ecosystem functioning. The European Commission's biodiversity (see box below) and soil strategies are designed to protect soils and their biodiversity while enhancing soil-based ecosystem services, with a view to promoting sustainable soil management. However, while we are gaining knowledge of the role of soil organisms in several processes that take place in soils, we have very little information about the geographical distribution and variation in soil biodiversity or the functional capacity of these belowground communities. [193]

The European Union project EcoFINDERS analysed soil biodiversity in 81 sites (orange dots) across Europe. The project involved 23 different research institutions from 12 European countries. (RCR, JRC)

In 2011, the EU Ecological Function and Biodiversity Indicators in European Soils (EcoFINDERS) project was launched to address this lack of spatial information on soils and to generate European datasets of soil biodiversity and ecosystem function. Soil biodiversity (microorganisms and fauna) were assessed at 81 sites across Europe: a sampling campaign of unprecedented scale for soil biodiversity. The sites cover a range of biogeographical zones, that include atlantic, continental, boreal, alpine and Mediterranean regions. Encompassed in these zones are a range of land uses: tillage, grass and forestry and a large spectrum of soil properties (represented by pH, organic carbon, total nitrogen and texture).

Standardised biological methods were applied to assess the abundance, diversity and functional capacity of organisms found in soils across Europe. These methods were selected for:

- their ability to provide relevant information, their cost-effectiveness
- their applicability in the field (at time of sampling) and laboratory (during analysis)

The diversity of archaea, bacteria, fungi, arbuscular mycorrhizal fungi, nematodes, enchytraeids, mites and collembolans were analysed (see Chapter II).

The data collected provide information to policy makers and land managers for establishing diagnoses of soil quality and designing practices for sustainable land management in order to preserve and value soil biodiversity. Furthermore, all samples being georeferenced will allow for the assessment of temporal variations of soil biodiversity across Europe resulting from global changes and human activities.

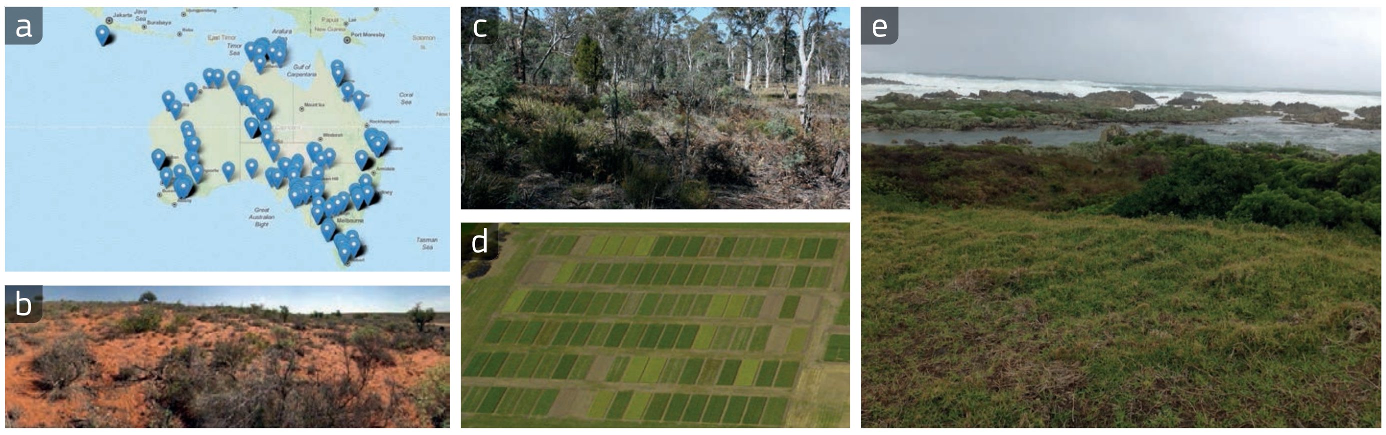
More details about EcoFINDERS can be found at the following link:

http://ecofinders.dmu.dk/

Biomes of Australian Soil Environments

The Biomes of Australian Soil Environments (BASE) programme is a collaborative effort initiated by the scientific community to develop a publicly accessible database that encourages the discovery and observation of soil microbial communities across Australia's diverse natural and agricultural ecosystems. The programme delivers a 'National Framework Dataset' that provides baseline information on microbial communities from Australian soils, and allows for the exploration of the determinants of these microbial properties at a continental and, ultimately, global scale.

The BASE database comprises microbial and environmental data collected in a systematic and controlled way to ensure reproducibility and inter-sample comparability. Information on the workflow including sampling strategy, DNA extraction, sequencing and physical and chemical analyses can be found on the BASE project portal (see https://ccgapps.com.au/bpa-metadata/base/information for details). All data collected by the project are publicly available via this portal, enabling identification of samples of interest and exploration of associated environmental data.



(**a**) Position of BASE sites with examples of biomes sampled; (**b–c**) represent National Reserve sites and (**d–e**) represent agricultural sites (FRE, PM).

Scientists from Bioplatforms Australia (BPA), Western Australian Department of Environment and Conservation (DECWA), Department of Economic Development (DEDJTR) in Victoria, several universities and research and development corporations CSIRO and the Director of National Parks (DNP) are participating in this effort to build a robust and accessible dataset of soil biodiversity information. The National Reserve System, long-term agricultural monitoring sites and the national ecological monitoring sites provide broad coverage of Australia's diverse biomes, geographic regions (tropical, subtropical, temperate, polar) and soil types.

The main aims of the BASE programme are to:

- quantify, compare and contrast soil microbial biodiversity and ecological function in a diverse range of Australian biomes
- develop a national framework for ongoing large-scale data collection that incorporates standardised microbial and environmental sampling and analysis protocols
- provide a baseline dataset for modelling relationships between soil microbial communities and vegetation, land use, climate, soil type and management
- examine the importance of microbes in generating ecological complexity, stability and resilience
- describe the role of microbes in plant productivity, mineralogy and general soil health
- inform the restoration of soil communities as part of plant revegetation and soil remediation strategies
- inform global biodiscovery

The repository contains microbial genome data comprised of bacterial and archaeal DNA sequences and fungal and other eukaryotic sequences (see pages 64-65). Each sample has associated edaphic variables (moisture, soil particle size, ammonium and nitrate content, total nitrogen, phosphorus, potassium, sulphur, total carbon, organic carbon, conductivity, pH, copper, iron, manganese, zinc and exchangeable cations and soil particle size) as well as non-edaphic site variables (elevation, slope, aspect), regional climate variables, overlying plant community composition and detailed land-use history.

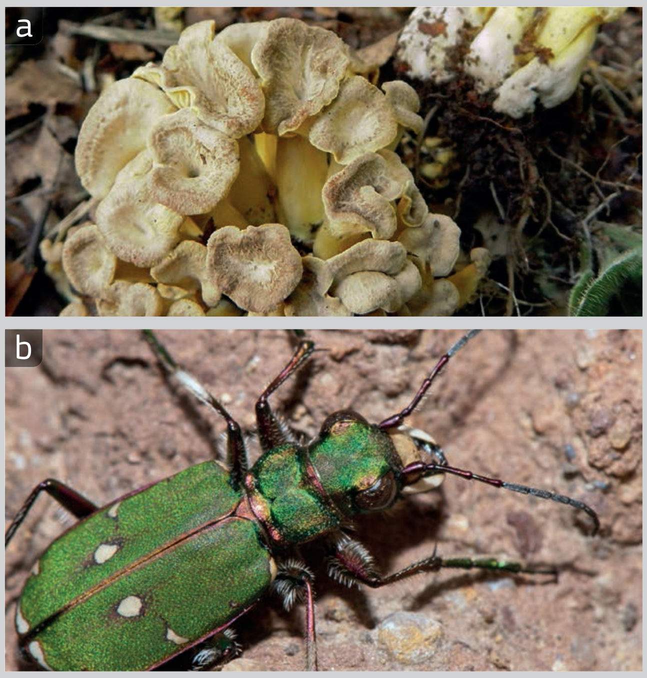
Visualisation of soil biodiversity data is also being developed in collaboration with the Atlas of Living Australia (www.ala.org.au) which provides a useful set of tools to visually describe the spatial distribution of soil biodiversity and the association between below- and aboveground terrestrial diversity. This framework database of soil microbial diversity is a valuable and enduring resource for scientists and the wider community. Insights into the current status of soil microbial diversity across a diverse range of Australian biomes relative to global soil biomes and the potential for future exploration of features presently unknown represent powerful drivers for ongoing participation in the BASE programme. More details about the BASE project, including the list of the 21 collaborating partner organisations, can be found at the following link:

www.bioplatforms.com/soil-biodiversity/

The BASE project could be a model for similar assessments of other continents, to eventually derive a global overview of soil biodiversity.

The European Union's Biodiversity Strategy to 2020

- In May 2011, the European Union adopted a new strategy to halt biodiversity loss in the EU, restore ecosystems where possible, and step up efforts to avert global biodiversity loss. The strategy is in line with the commitments made by EU leaders in March 2010 and the international commitments adopted by 193 countries, including the EU and all its Member States, at the Conference of the Parties to the Convention on Biological Diversity in Nagoya (Japan) in 2010.
- The biodiversity strategy is built around six measurable targets that focus on the main drivers of biodiversity loss. The six targets cover:
  - full implementation of EU nature legislation to protect biodiversity;
  - better protection for ecosystems, and more use of green infrastructure;
  - more sustainable agriculture and forestry;
  - better management of fish stocks;
  - tighter controls on invasive alien species;
  - larger EU contribution towards averting global biodiversity loss.
- Each target is accompanied by a corresponding set of actions. The main challenges ahead include the full and efficient implementation of nature protection legislation – especially the effective management and restoration of areas of high biodiversity value in Natura 2000, tackling invasive alien species and protecting ecosystem services.



Species native to Europe are linked to soil, such as (**a**) the fungus *Cantharellus melanoxeros* and (**b**) the green tiger beetle *Cicindela campestris* (BCL, JBA)

Knowledge sharing

Participatory research

The increasing global awareness of the impacts of biodiversity loss on human well-being has created great concern and demands for rapid action. Agriculture is the most widespread form of human-environment interaction. Farmers, therefore, constitute the largest group of natural resource managers on Earth. [194]

The increasing attention paid to farmers' knowledge recognises that experience gained during years of direct interaction with nature can offer many insights into the sustainable management of natural resources. Soil health is an important indicator of the state of natural capital. It reflects the capacity of soil to function as a vital living system and respond to agricultural management by sustaining the biological productivity that underpins the provision of food and fibre, as well as other ecosystem services. Soil health is of great concern to farmers, particularly resource-poor smallholder farmers who rely to a large extent on the biological productivity of soil to sustain their livelihoods.

Blending local and technical knowledge leads to an expanded shared knowledge that is more relevant and credible. (**a**) Farmers share with researchers the relative importance of different local indicators of soil quality in Nampula, Mozambique. (**b**) A farmer training session in the village of Chapor, in Bangladesh. (EB/ICRAF, SMO/DRI/CIMMYT)

Smallholder farmers around the world have developed a number of detailed local soil classification systems based on years of observations and a variety of soil health indicators. Dominant plant species and earthworms are important indicators commonly used by farmers across different continents for visual characterisation of soil health during selection of areas for agriculture. Above- and belowground biodiversity are closely tied to aspects of soil health, making it possible to use the presence, absence and abundance of species as biological indicators. Increasing efforts in participatory research are currently being promoted in order to foster the integration of local knowledge into soil health monitoring systems and thus support decision-making processes aimed at the sustainable management of natural resources in agricultural landscapes.

While local and technical knowledge share a number of common 'core' concepts, each knowledge system has gaps that in many cases can be complemented by each other. Blending local and technical knowledge aims to generate an expanded 'shared' knowledge that is more sound and credible, thus facilitating the adoption of agricultural management practices that conserve soil biodiversity.

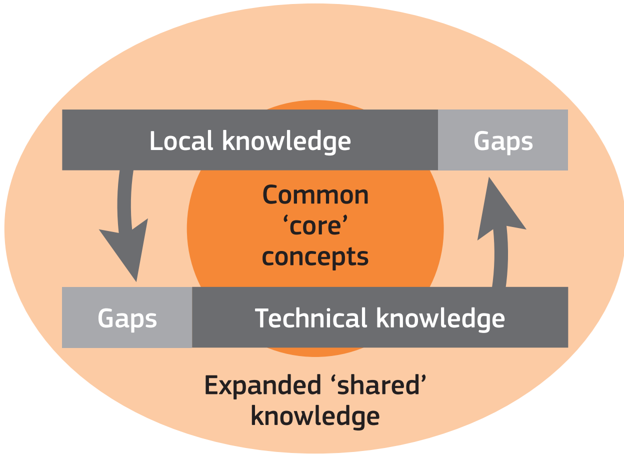


Illustration showing that farmers' knowledge and scientific knowledge share a number of common core concepts, but each knowledge system has gaps that in many cases can be complemented by each other. An integration of the two knowledge systems is needed to obtain a shared knowledge (derived from Barrios *et al.*, 2012). [194]

Soil biodiversity awareness in Honduras

- A participatory research scheme was carried out in an agroforestry system of western Honduras in order to assess the extent to which farmers have incorporated their local knowledge into farm management practices. [195]
- The local knowledge of twenty small scale farmers was identified, classified and prioritised through a number of participatory research tools. Farmers named 16 commonly recognised, distinct groups of soil macrofauna. In addition, they distinguished several local soil types on the basis of soil texture, colour and structure.
- The most detailed knowledge of the relationship between soil fauna and soil quality was on organisms considered to have either beneficial or harmful effects on farming activities, such as earthworms and beetle larvae (see pages 58-60).
- Farmers had a clear understanding of the influence of fire on soils, soil biota, native vegetation and crop yield over various lengths of time, which may have been obtained through a combination of first-hand experience, interaction with technical experts and information gained from other farmers.
- Researchers concluded that local knowledge of the effect of different soil organisms on soil quality, the interactions among them and the role of native vegetation in maintaining agricultural productivity, is an important driver of the success of the agroforestry system.

A better understanding of soil biodiversity allows small farmers in Honduras to manage their land in a more sustainable way. The photograph shows a nursery of tree seedlings which will be planted to restore degraded land. (TFTF)

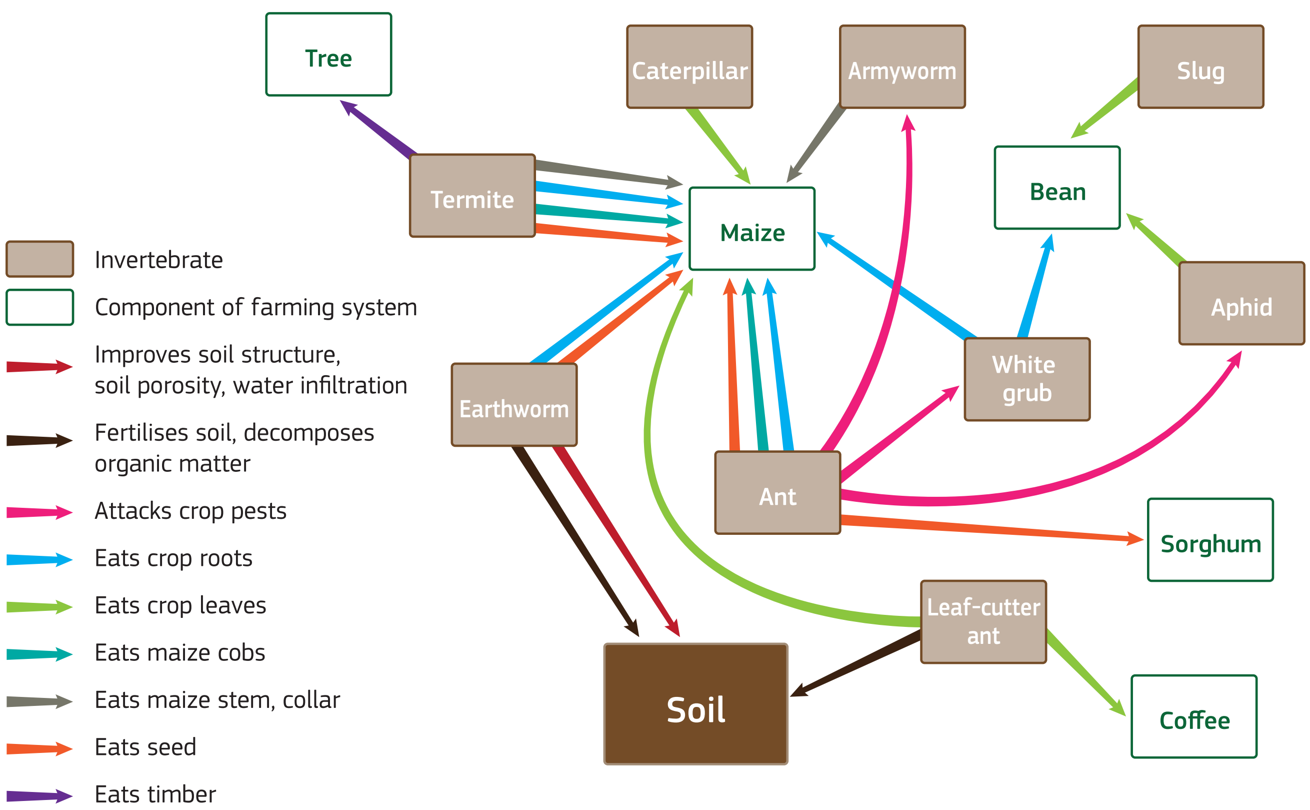


Illustration of farmers' perceptions of the effect of soil invertebrates on components of the farming system (derived from Pauli *et al.*, Geoderma, 2012). [195]

Citizen science

Other forms of knowledge sharing through participatory research, which extend beyond agricultural landscapes into natural ecosystems, include citizen-science efforts that have become increasingly common in the past decade. Citizen science can be defined as the participation of volunteers from the public in scientific research. It is considered an effective ecological research tool to increase our understanding of processes occurring at broad geographical scales.

For example, the Great Lakes Worm Watch is a US citizen-science effort to assess the impact of exotic earthworms on forest ecosystem processes [196]. Interested citizens are provided with tools and resources to actively contribute to the development of a database that documents the geographic and spatial distribution and abundance of exotic earthworms, as well as their environmental impact. The Open Air Laboratory (OPAL) network (www.opalexplorenature.org) is a broader citizen science initiative in the UK aimed at increasing public awareness of the state of the environment through direct experience.

Changes in public perceptions about the importance of the conservation and management of natural resources achieved through experiential learning aims to guide civil society toward more sustainable development pathways and also influence environmental policy.

(**a**) Citizen science is a valuable source of data for the scientific community. (**b**) See below how to collect earthworms. (PCR, JRE)

Make your earthworm survey

The Open Air Laboratory (OPAL) network provides a kit and all the instructions needed to survey earthworms [197]. The results will help scientists to see whether each species is found in a particular habitat or soil type. For example, there are 26 different species of earthworms in England. Some are common and found in many places, whereas others are rare. Earthworms are sensitive to many environmental factors, which influence where they live. If you find many earthworms in your soil it can be a sign of good soil quality.

Steps and materials needed to sample are very simple and can be found on the OPAL website. Essential items to take outside are:

1. magnifier
2. mustard
3. vinegar
4. 2 pH strips
5. two 750 ml bottles of water (re-use old plastic bottles filled with tap water)
6. a small shovel, spade or trowel
7. gloves
8. a map and GPS device, if available
9. waterproof pen
10. a mobile phone
11. a camera
12. a watch

Following the simple instructions proposed by the Open Air Laboratory for sampling earthworms helps to actively improve knowledge of earthworms and the soils in which they live. (OPAL)

When the material is ready:

a. choose a location and record the site characteristics (e.g. weather and vegetation cover)

b. measure a 20 x 20 cm square, dig the soil pit to a depth of 10 cm and apply a mixture of water and mustard to extract deep worms

c. test the properties of the soil (e.g. pH and moisture). Simple instructions to describe these aspects are provided; for example, to test soil moisture it is sufficient to take a handful of soil in the palm of your hand and squeeze it, if water is visible the soil can be considered as wet

d. identify the earthworms. Also in this case keys and hints to identify earthworm species are provided. For example, 12 of the most common earthworm species in England are illustrated in the key. The key should identify approximately 90 % of adult specimens. Immature worms cannot be identified but people should still record the total number found in the topsoil and deeper in the pit using the mustard water. The use of a magnifier can help you see key earthworm features (this will help with species identification). Furthermore, a digital camera can be used for identification by taking a picture and zooming in to see the details

e. enter all results on the OPAL website

This example clearly shows the feasibility of participatory research initiatives. These activities can have a double positive effect. Firstly, to enhance awareness of the importance of soil biodiversity and, secondly, to actively contribute toward scientific research.

An amazing story to share!

- There are several anecdotes related to organisms living in the soil or associated with soil, which should be shared in order to increase awareness of the importance and beauty of soil biodiversity.
- *Osmia avosetta* is a rare and solitary species of bee from Iran and Turkey, that makes flower-mud 'sandwiches' to construct nests for its larvae. [198]
- The female *Osmia avosetta* digs shallow tunnels in the ground consisting of one or two chambers, each of which it then lines with flower petals glued together with mud.
- It then places larval food in each chamber and seals it with soil by folding the petals over. The cell hardens to form protection for the larva against predation and weather.
- The reason for the effectiveness of these elaborate nests is the texture, water content and water repellency of the soil used by the bee and the humidity-retaining nature of the petals.
- The colourful nesting behaviour of *Osmia avosetta* bees was discovered simultaneously in 2009 in Turkey and Iran.
- Similar to this bee, several species of bumble bees (*Bombus* spp.) are regarded as soil-dwelling insects since they build their nests in soil and are important pollinators (see box on page 61).

(**a**) Nest of the *Osmia avosetta* bee showing the shape and variation in colouration of the outer envelope. (**b**) Same nest, now with the top of the outer envelope removed to reveal the soil closure. (**c**) Open nest in a short cavity excavated in rather hard soil. (JGR, STH)

Education and awareness

Need for awareness

The main scope of this atlas is to educate and raise awareness about the importance of soil biodiversity. Scientific knowledge has been largely restricted to text books and scientific journals, which are often inaccessible and incomprehensible to the general public. Recently, there has been increased realisation of the need to engage society with scientific results in a manner that can be more easily understood. Interestingly, providing knowledge about soil biology is a very powerful way to introduce soil issues to the public.

The need to raise awareness and understanding of the importance of soil and soil biodiversity has been highlighted on a global scale. The more we can learn about the role that soil biota plays in sustaining the environment, the more we understand how important it is and, hopefully, the more likely we are to care for it.

Soil biodiversity playing cards

- A card game was designed and published in French under the GESSOL (*GEStion du patrimoine SOL*) research programme, funded by the French Ministry of Ecology, and in English by the European Commission's Joint Research Centre.
- This card game, 'The hidden life of soils', comprises 42 playing cards, each with a large photo and description of a group of soil organisms. This allows for discovery of the hidden organisms that inhabit the soil, how they live and how to study them.

Two of the seven happy families of soil organisms included in the card game. (GESSOL)

The cards can be downloaded at the following links:

http://www.gessol.fr/game-hidden-life-soils

http://esdac.jrc.ec.europa.eu/networkcooperations/educational-material-soils

Children love (**a**) drawing soil biodiversity and (**b–d**) playing with soil. Hands-on activities allow both children and adults to see soil biodiversity from different perspectives. (JRC, ACO, DAD, JPA)

Targets of awareness raising

It is important that we teach the importance of soil biodiversity to society at large, from young children, school teachers, farmers and gardeners to planners and politicians. Children love playing with soil and have the capacity to learn through simple hands-on activities, such as making mud pies, building wormeries and looking under the microscope at what lives in the soil.

Drawings made by children show their perception of soil and, perhaps surprisingly, such sketches or paintings often convey complex messages about issues such as the food chain or the importance of earthworms in increasing the pore network underground. These are lessons that scientists constantly strive to communicate. The ability to recognise ecological interactions, however, seems to be inherent to many children who are fascinated by life in the soil.

The following sectors also benefit from education and awareness:

a. higher education: the knowledge of soil in general, and soil biology and ecology in particular, is often neglected and should be integrated across disciplines
b. scientific community: should be made more aware of the importance of soil biodiversity. This can be achieved through a multidisciplinary approach where people specialised in different subjects cooperate and understand each other
c. farmers and land managers: farmers generally have a good relationship with the soil because it is the basis of their livelihood. The functions of the living soil system should be clearly communicated. Farmers should be part of the development of management options that are beneficial for soil biodiversity, which in turn can increase yields and reduce costs
d. policy makers and NGOs: should influence public opinion. Soil and related biodiversity usually has a low political priority. Increasing this awareness would contribute to informed decision-making processes that would bring enormous benefits through increased quality of life
e. public: public opinion is a powerful tool for changing societal attitudes toward the importance of soil. Increased education and awareness-raising campaigns must stress the value of soil biodiversity to people's daily lives

A coordinated approach is required in order to target each sector and to encourage interactions among them.

(**a**) Molly the Mole is the mascot of all soil awareness events organised by the European Commission's Joint Research Centre. (**b**) Sammy Soil is the mascot of the United States Department of Agriculture's Natural Resources Conservation Service. (GBA, LCH/USDA)

The good, the bad and the ugly!

Some soil organisms can either bite or sting and may become pests or promote diseases. However, unpleasant soil organisms represent a very small proportion compared to the huge amount of remaining soil organisms. Furthermore, pests and diseases are largely the result of a natural disequilibrium and/or environmental changes, often man-made, resulting in a population explosion of a given species, due to the disappearance of their natural enemies.

Many people have developed phobias to microbes and insects in general, considering them all bad and ugly. Therefore, education is required to show how they can be good and beautiful. Besides, our own lives would not be possible without them!

Curumin and *Cunhantã* helping soil biodiversity

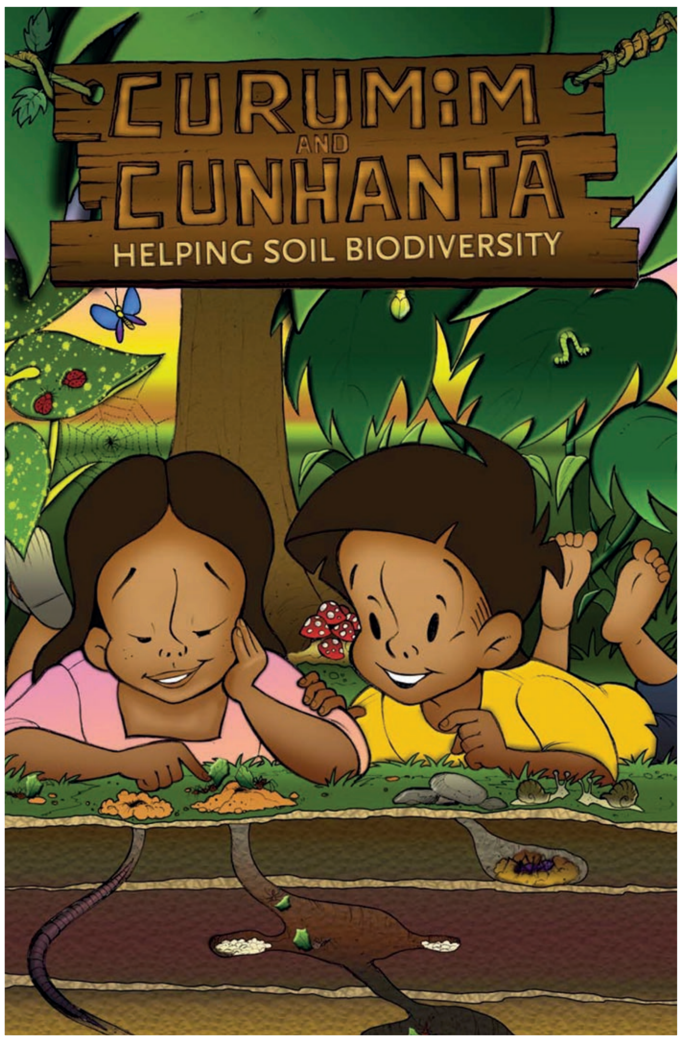
In the context of the Global Collaborative Project entitled 'Conservation and Sustainable Management of Belowground Biodiversity', the Brazilian Federal University of Lavras (UFLA) developed an educative booklet to explain the importance of soil biodiversity. Entitled 'Curumim and Cunhantã helping soil biodiversity', the booklet is available in Portuguese, Spanish and English.

Curumim and Cunhantã means boy and girl in a Brazilian native language. Regardless of gender, scientists and children share a common trait: curiosity, which is the stimulus and motivation for science. The booklet tells a story about the importance of soil biodiversity. This story is told by characters based on the Brazilian scientists that worked in the area of a research project in Amazonia, and illustrated with results found there, such as soil type, soil limiting factors, number of plants, and a few key macrofauna (e.g. earthworms) and microbial (e.g. bacteria) species.

Soil biodiversity is presented in an holistic way considering its physical and chemical attributes (soil fertility) and its effects on plant productivity. The value of soil organisms is highlighted by considering them as true super heroes because in nature their activities are real and they help plants, ecosystems and human beings live on planet Earth. This is the reason why we need to help preserve them. The booklet is not only about soil biodiversity, but also about human diversity and how these diversities can help each other.

The booklet can be downloaded at this link:

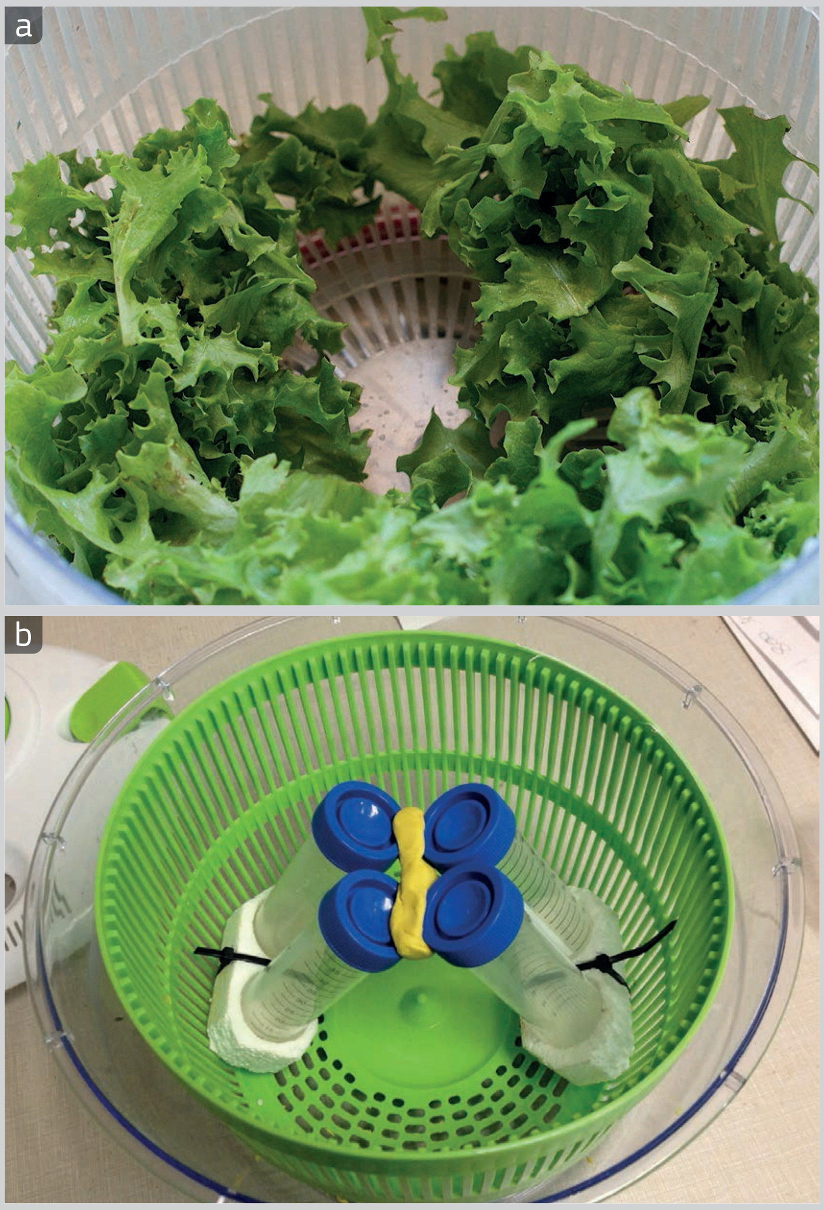
http://repositorio.ufla.br/handle/1/1476



The booklet *Curumim and Cunhantã* presents soil biodiversity through a simple language and can be used as an educational tool to illustrate soil life. (UFLA)

A homemade centrifuge to explore soil biodiversity

- For a simple outreach activity, a working low-speed (around 900 revolutions per minute) centrifuge can be easily made using a household salad spinner.
- Styrofoam bases from 50 ml centrifuge tube packs are secured to the bottom of a salad spinner using zip-ties. Putty/modelling clay is used to stabilise the centrifuge tubes. Wrapping a rubber band around the tops of the tubes provides additional stability during spinning.
- Use hand trowels to collect approximately 100 ml of soil, mix it with tap water in a bucket, and let the sediment settle for 1 minute before pouring the solution through large (1 mm) and fine (< 1 mm) mesh soil sieves.
- Use squirt bottles to gently wash the material caught on the fine mesh sieve into a 50-ml centrifuge tube, and hand-spin tubes in the salad-spinner centrifuge for 5 minutes. Up to four tubes could be spun at once.
- Remove the tubes and empty the liquid, while retaining the loose soil pellet at the bottom of the tube containing soil organisms, such as mycorrhizal spores and nematodes.
- Refill the tubes with 60 % sucrose (table sugar) solution, cap and invert the tubes a few times to mix, and put back in the salad-spinner centrifuge for another 3-4 minutes. Soil organisms will float in the sugar water while mineral components sink.
- Pour the sugar water solution through the fine- mesh sieve while leaving the mineral pellet in the tube, and gently wash the sieve with tap water to remove sugar residues from organisms.
- The material left in the sieve could then be gently washed into small dishes for observation under microscopes. While the samples remain dirtier and less quantitative than what is possible using higher-speed electric centrifuges, small living soil organisms are clearly visible.



It is easy to make a centrifuge, you just need (**a**) a salad spinner, (**b**) two styrofoam bases with two holes each, and four tubes. (ALE, SMM)

Soil biologist for one day

Soil biodiversity can be easily studied with simple equipment. While bacteria, fungi, microfauna (< 0.1 mm, e.g. nematodes) and mesofauna (0.1 to 2 mm, e.g. mites) require special techniques to be isolated and extracted from soil, macrofauna (> 2 mm, e.g. earthworms) can be extracted from soil samples using methods accessible even to children.

A simple method to show visible soil organisms and compare the effect of diverse soil conditions (e.g. forest versus prairie, clay soil versus sandy soil) is described below:

1. delineate a square on the soil surface (e.g. 25 × 25 cm)
2. dig around this area to a given depth (e.g. 10 cm) in order to have an isolated block of soil
3. carefully lift this block of soil (25 × 25 × 10 cm) and place it on a tray
4. put on gloves, take out all the small animals that you can see moving and place them in a vial with alcohol. You can use tweezers; however, take care to avoid crushing them. Smaller animals can be collected with a wet paint brush
5. when you are sure that all animals have been removed, they can be counted and viewed under a simple microscope or magnifying glass. Beautiful forms of life invisible to the naked eye will be revealed and children will discover new creatures
6. if needed, the procedure can be repeated for deeper layers (e.g. 10 to 20 cm) and the results compared

The diversity of soil organisms can be evaluated by simply separating them by shape and size. Numbers and types of individuals will differ according to soil types and habitats. Children can also draw the ones they like most.

The presented activities are just a small sample of the myriad activities (see pages 164-165) that can be proposed not only to children but also students and adults in order to raise awareness of the diversity of soil life and the importance and fascination of studying soil-living organisms.

Being a soil biologist for a day is easy. (**a**) Dig a hole, take out the small animals that you can see and (**b**) place them under the microscope: (**c**) an astonishing world will appear before your eyes. (FMSM, DSE, MN)

Resources

Learning about soils and soil organisms

Often the best place to teach people about soils is to go into a field, a woodland or just a garden. In these environments, students can investigate for themselves the soil biodiversity and the role it plays in keeping our environment alive. Simply digging a small hole, lifting stones to see what lies underneath, sifting through plant litter or just setting a few pitfall traps made from yogurt containers will quickly bring you into contact with soil biota. The use of magnifying lenses or microscopes to show the variety of soil organisms found in a few grammes of soil is a simple lesson, guaranteed to leave a long-lasting impression. A huge amount of educational material is becoming available for both students and teachers. This includes computer programmes, lesson plans, supporting materials and activities for both the classroom and outdoors. The great thing about teaching soil biology is that it is applicable across all ages from young children who make wormeries, to school and university students who discover the importance of soil biology in the global nutrient cycles and ecosystem functions. A number of promising educational initiatives have been developed for the general public and, in particular, for children to learn outside of the school environment. Examples include interactive museums or informative nature walks that tell the story of soil and its role within a particular landscape. Another interesting method is to use images of creatures that live in the soil to help raise public awareness of the importance of life in soil. These examples show very clearly that soil organisms can compete with other, perhaps more well-known and charismatic, animals such as elephants and lions, in raising awareness of soil biodiversity. Here below you will find a list of resources on soil and its biodiversity.

Web links

- Biodiversity International: www.bioversityinternational.org
- Centre for Soil Ecology: www.soilecology.eu
- Digital Atlas of Actinomycetes: http://atlas.actino.jp/
- Earth Microbiome Project: www.earthmicrobiome.org
- European Land and Soil Alliance: www.bodenbuendnis.org
- European Network on Soil Awareness: www.bodenbuendnis.org/ensa/ and www.hutton.ac.uk/events/european-network-soil-awareness
- European Soil Portal: http://esdac.jrc.ec.europa.eu/
- Global Soil Biodiversity Initiative: www.globalsoilbiodiversity.org
- Food and Agriculture Organization – Global Soil Partnership: www.fao.org/globalsoilpartnership/en/
- GEStion du patrimoine SOL: www.gessol.fr
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services: www.ipbes.net
- International Year of Soils: www.fao.org/soils-2015/en/
- Life Under Your Feet: http://lifeunderyourfeet.org
- Natural Resources Conservation Service: www.nrcs.usda.gov/wps/portal/nrcs/main/national/soils/health/
- Soil is Life: www.soil-is-life.info/content_en/index.htm
- Soil Science Society of America: www.soils.org and www.iheartsoil.org
- Soil Science Teacher Resources. www.soils4teachers.org
- SoilGrids 1km visualisation: www.soilgrids.org
- SoilInfo App: http://soilinfo-app.org
- Soil-net: www.soil-net.com/
- Soils 4 Kids: www.soils4kids.org
- TerraGenome: www.terragenome.org
- The British Society of Soil Science: www.soils.org.uk/
- The Convention on Biological Diversity: www.cbd.int
- The Dirt on Soil – Learning Adventures: http://school.discoveryeducation.com/schooladventures/soil/
- Tool for Research Engaged Education: www.tree.leeds.ac.uk/tree_home.php
- Virtual Soil Science: http://soilweb.landfood.ubc.ca/promo/raising-awareness
- Wageningen Soil Network: www.wageningenur.nl/en/article/Year-of-Soils.htm
- World Soil Museum: www.isric.org/services/world-soil-museum
- Soil protists: https://soilprotists.wordpress.com

Facebook and Twitter

- Bundesverband Boden e.V.: ww.facebook.com/BundesverbandBoden
- Che Terra Pesti: www.facebook.com/cheterrapesti
- Global Soil Biodiversity Inititiative: @theGSBI
- Plants, Soils, Ecosystems Group: @BESPlantSoilEco
- Soil Science Society of America: www.facebook.com/SSSA.soils

Blogs

- Beneath Our Feet: http://blog.globalsoilbiodiversity.org
- Observerland: http://observer.land/

Summer schools

- Plan-it Earth: www.plan-itearth.org.uk
- Summer of Soil: www.summerofsoil.se
- Summer Soil Institute at Colorado State University: http://soilinstitute.nrel.colostate.edu/

E-learning

- Allversity – Understanding Soil: http://www.allversity.org/courses/understanding-soil
- Science Learning Hub: http://sciencelearn.org.nz/Contexts/Soil-Farming-and-Science

In these pages you will find links and much more to learn about soil. (LRI)

A page from the 'I Love Soil Coloring and Activity Book' by the Soil Science Society of America. Go ahead and colour this page! (SSSA)

Movies, arts and more

- A story with heart and soil: www.dirtthemovie.org
- Common Ground: www.commonground191.com
- Dig in! Diners served food made from SOIL at top Japanese restaurant: http://www.dailymail.co.uk/news/article-2451089/Ne-Quittez-Pas-Japanese-diners-served-soil-based-dishes-restaurant.html#ixzz3Wc93lBQl
- New film festival strives to raise awareness of soil sustainability: www.iowastatedaily.com/news/article_dff5cd4a-315a-11e4-aa41-001a4bcf887a.html
- Painting With Soil: http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/edu/7thru12/?cid=nrcs142p2_054304
- Poem: Marking World Soils Day 2014: www.farmersjournal.ie/poem-marking-world-soils-day-2014-170544/
- Soil Arts: http://soilarts.wordpress.com/
- Soil Biodiversity: www.youtube.com/watch?v=oXddZCcIla8
- Soil Culture: http://vimeo.com/112804613
- Soilscape Studio: http://soilscapestudio.com/paintings.htm
- Song 'Amazonia: a happy soil': www.youtube.com/watch?v=lwQ0R-iBK_s
- Symphony of the Soil: www.symphonyofthesoil.com
- Tea Bag Index: www.decolab.org/tbi/
- The Secret's in the Soil – Modern Farmer interviews the world's pioneer of 'soil cuisine' Toshio Tanabe: http://modernfarmer.com/2013/10/secrets-soil/
- Workshop: Making Paint from Soil: http://parideazafarmart.wordpress.com/workshop-on-making-paint-from-soil/

Scientific articles

- Bindraban, P.S., *et al.*, 2012. Assessing the impact of soil degradation on food production. Current Opinion in Environmental Sustainability 4: 478-488.
- Bouma, J., *et al.*, 2012. Soil information in support of policy making and awareness raising. Current Opinion in Environmental Sustainability 4: 552-558.
- Gülay, H. *et al.*, 2011. Children in need of protection and learning about the soil: A soil education project with children in Turkey. Procedia – Social and Behavioural Sciences 15: 1839-1844.
- Hartemink, A.E., *et al.*, 2008. Trends in soil science education: Looking beyond the number of students. Journal of Soil and Water Conservation 63: 76A-83A.
- Hassenpflug, W., 1998. Creating 'soil awareness' – A neglected task of geography teaching. Erde 129: S53-S61.
- Levesley, A., *et al.*, 2014. Engaging students with plant science: the Plant Science TREE. New Phytologist 203: 1041-1048.
- Megonigal, P.J., *et al.*, 2010. 'Dig It.': How an exhibit breathed life into soils education. Soil Science Society of America Journal 74: 706-716.
- Muggler, C.C., *et al.*, 2006. Soil education: Principles, theory and methods [Educação em solos: Princípios, teoria e métodos].Revista Brasileira de Ciencia do Solo 30: 733-740.
- Ogelman, H.G., 2012. Teaching preschool children about nature: A project to provide soil education for children in Turkey. Early Childhood Education Journal 40: 177-185.
- Schmidt, C.W. 2006., Putting the earth in play: Environmental awareness and sports. Environmental Health Perspectives 114: A286-A295.
- Weyer, T., Boeddinghaus, R., 2013. Soil compaction and soil protection. Geographische Rundschau 65: 28-35.
- Yaalon, D.H., 1996. Soil science in transition: Soil awareness and soil care research strategies. Soil Science 161: 3-8.

The Youth & United Nations Global Alliance (YUNGA) booklet on soils. (YUNGA)

Journal articles

- National Portrait Gallery installation will transform tonnes of sand and soil on the Mall: www.washingtonpost.com/lifestyle/style/national-portrait-gallery-installation-will-transform-tons-of-sand-and-soil-on-the-mall/2014/08/18/08813be8-270e-11e4-8593-da634b334390_story.html?tid=hpModule_ef3e52c4-8691-11e2-9d71-f0feafdd1394&hpid=z14
- Our Good Earth – The future rests on the soil beneath our feet: http://ngm.nationalgeographic.com/2008/09/soil/mann-text
- Sex & Bugs & Rock 'n Roll: http://planetearth.nerc.ac.uk/features/story.aspx?id=1671&cookieConsent=A
- Soil Health Campaign Turns Two: Seeks to Unlock Benefits on- and off-the-Farm: http://blogs.usda.gov/2014/10/10/soil-health-campaign-turns-two-seeks-to-unlock-benefits-on-and-off-the-farm/
- The Dirt on Dirt: 5 Things You Should Know About Soil: http://news.nationalgeographic.com/news/2014/12/141205-world-soil-day-soil-agriculture-environment-ngfood/?utm_source=NatGeocom&utm_medium=Email&utm_content=foodiefri_20141212&utm_campaign=Content
- The Hidden World Under Our Feet: http://www.nytimes.com/2013/05/12/opinion/sunday/the-hidden-world-of-soil-under-our-feet.html?pagewanted=all&_r=1&

Movies, articles, photos and even games and calendars. Online there is plenty of material about soil and its biodiversity. (USDE)

'I Love Soil' campaign by the Soil Science Society of America. (SSSA)

- The importance of the soil: http://ruhlman.com/2014/05/the-importance-of-the-soil/

Videos and radio

- BBC Inside Science: www.bbc.co.uk/programmes/b04xrwhc
- Flight through the pore network of a 1 mm soil fragment: www.youtube.com/watch?v=7fhufJHzGsM&feature=player_embedded
- Forces of Change: http://forces.si.edu/soils/video/secret_ingredient.html
- Nature Is Speaking: http://natureisspeaking.org/thesoil.html
- Plant-soil feedbacks after severe tornado damage: http://vimeo.com/107412178
- Worms at Work: http://vimeo.com/110880643

Books

- A World in One Cubic Foot: Portraits of Biodiversity. 2012. David Liittschwager. The University of Chicago Press. ISBN: 978-0226481234.
- Dirt. 2007. Steve Tomecek and Nancy Woodman. National Geographic Children's Books. ISBN: 978-1426300899.
- Ecology, Soils, and the Left – An Ecosocial Approach. 2014. Salvatore Engel-Di Mauro. Palgrave Macmillan. ISBN: 9781137350138.
- Reflections on the Basis of our Existence. 2014. Håkan Wallander. Springer Edition. ISBN: 978-3319084572.
- Soil Atlas: Facts and figures about earth, land and fields. 2015. Edited by Christine Chemnitz and Jes Weigelt. Heinrich Böll Foundation, Berlin, Germany. http://globalsoilweek.org/soilatlas-2015
- Soils Challenge Badge. 2014. The Youth & United Nations Global Alliance: http://www.fao.org/3/a-i3855e.pdf
- The Soil Will Save Us. 2014. Kristin Ohlson. Rodale Books. ISBN: 978-1609615543.

Calendar

- Calendar 2015 – Soil functions: keeping the Earth alive http://eusoils.jrc.ec.europa.eu/Awareness/Documents/Calendar2015/Calendar2015.pdf

Games

- I Love Soil Coloring and Activity Book: https://www.soils.org/files/iys/iys-colorbook-for-web.pdf
- Soil memory: http://memo.geo-learning.de/modules/memo/lbeg.html
- Soil Fauna Playing Cards: www.gessol.fr/game-hidden-life-soils
- Soil Horizon Game: http://forces.si.edu/soils/swf/hiddenhorizons.html
- Where in the World? http://forces.si.edu/soils/swf/whereintheworld.html

Photos

- Our Good Earth – Jim Morrison, National Geographic: http://ngm.nationalgeographic.com/2008/09/soil/richardson-photography

Science communication

- Center for Public Engagement with Science & Technology: www.aaas.org/pes
- Lisode – Lien Social et Decision: www.lisode.com/home/

Global Soil Biodiversity Initiative

The Global Soil Biodiversity Initiative (GSBI) was launched in Wageningen in 2011 to make better use of our understanding of soil biodiversity. The GSBI is developing a coherent platform in order to promote the translation of expert knowledge into environmental policy and sustainable land management practices, ultimately resulting in better protection and enhancement of ecosystem services. Soils are home to a vast diversity of life that is essential for a variety of ecosystem functions – from the tiniest microbes to larger soil animals and plant roots. Yet soil biodiversity has been largely ignored in global and regional policies addressing land management, food security, climate change, loss of biodiversity and desertification.

Scientific priorities for the GSBI include identifying key knowledge gaps linking soil biodiversity and ecosystem function, developing a platform for the synthesis of soil biodiversity data, methods harmonisation, establishing a forum for global research networks and supporting international soil biodiversity research initiatives and soil-related policy agendas.

The GSBI aims to integrate soil biodiversity science with ongoing global scientific efforts, such as the Global Soil Partnership (GSP), the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) and the Convention on Biological Diversity (CBD). It will enhance soil biodiversity options and identify ways to restore, conserve and promote it, and is open to all scientists, land managers, policy makers and the general public. The GSBI is working to:

- inform policy-making and research by providing clear, transparent and scientifically credible information
- collaborate with existing and new initiatives on biodiversity that relate to soil
- encourage capacity building in all aspects of soil biodiversity and ecosystem services

Leadership

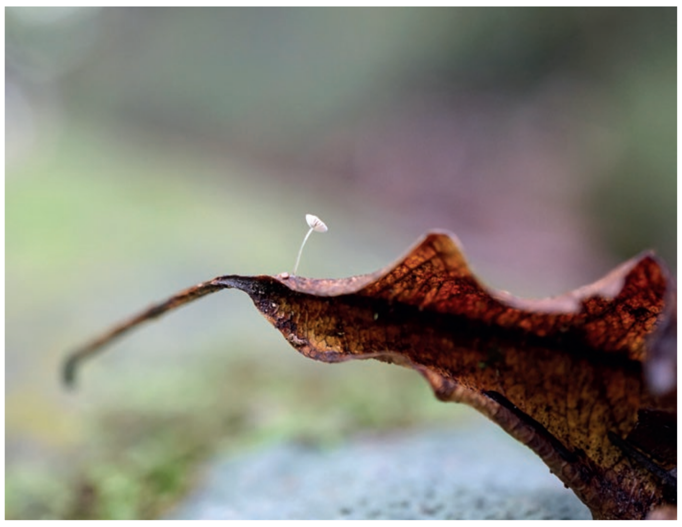
The GSBI is led by an international scientific steering committee, with the Secretariat office hosted at the School of Global Environmental Sustainability, Colorado State University, United States of America. Members of the committee are:

- Diana H. Wall – Scientific Chair, Colorado State University, USA
- Executive Director – Person covering this position changes every three years, Colorado State University, USA
- Ciro Gardi – Scientific Program Coordinator, European Food Safety Authority, Italy
- Fred Ayuke – University of Nairobi, Kenya
- Richard D. Bardgett – University of Manchester, UK
- Nobuhiro Kaneko – Yokohama National University, Japan
- Luca Montanarella – European Commission's Joint Research Centre, Italy
- Fatima M. S. Moreira – Federal University of Lavras, Brazil
- Johan Six – ETH Zurich, Switzerland
- Wim H. van der Putten – Netherlands Institute of Ecology, the Netherlands

Participation

The GSBI aspires to be a truly global initiative. In October 2015, more than 800 members representing 88 countries had signed up as participants, although some parts of the globe continue to be largely under-represented. This international community provides a reservoir of specialists globally and regionally, contributes to scientific updates and policy actions, and ensures that all aspects of soil biodiversity and ecosystem services are addressed. The GSBI communicates information through email, social media and the website:

www.globalsoilbiodiversity.com



The Global Soil Biodiversity Initiative was designed to foster global collaboration among scientists, all with the goal of informing the public, promoting the inclusion of this information into environmental policy and creating a platform for the current and future sustainability of soils and their biodiversity, from microorganisms to megafauna. (AH)

GSBI Activities

The GSBI engages the public and policy sectors through its numerous activities and provides a forum to enhance global sustainability efforts. Existing initiatives by GSBI participants include the early-career scientists creating a network of emerging scientists from around the world, an urban working group to highlight the importance of soil organisms in populated areas, a group interested in the social and cultural values of soil biodiversity and an education section to establish creative methods to deliver this information to a wider audience of all ages. In addition, networking among different groups specifically interested in protists, soil fauna and functional groups across all soil taxa are being established.

Since soil biodiversity data can be used to address questions ranging from ecosystem function to global biodiversity to global change, a Soil Biodiversity Curation Working Group was established to bring together all soil biodiversity data on taxonomy, phylogeny and function. This group hopes to:

- provide access to soil biodiversity databases, data sources and related information (discoverability)
- promote the use of standards – provide guidelines, best practice policies, promotion of use
- establish a framework to bring together past, present and future soil biodiversity data and related information (for minimum and optimal uses)

The First Global Soil Biodiversity Conference

On 2 December 2014, more than 700 scientists and interested parties from 57 countries gathered in Dijon, France for the first 'Global Soil Biodiversity Conference – Assessing soil biodiversity and its role for ecosystem services'.

Organised by the GSBI, the EcoFINDERS project, the European Commission and the French National Institute of Agricultural Research (INRA) Dijon, the conference was designed as a platform to discuss current research in soil biodiversity and its links to Earth processes, and to promote interdisciplinary collaboration. The conference included 13 keynote speakers, 46 oral presentations and 666 poster presentations. On the final day of the conference, a panel discussion brought together government officials, senior scientists and early-career scientists in celebration of World Soil Day (5 December) and the launch of the 2015 International Year of Soils.

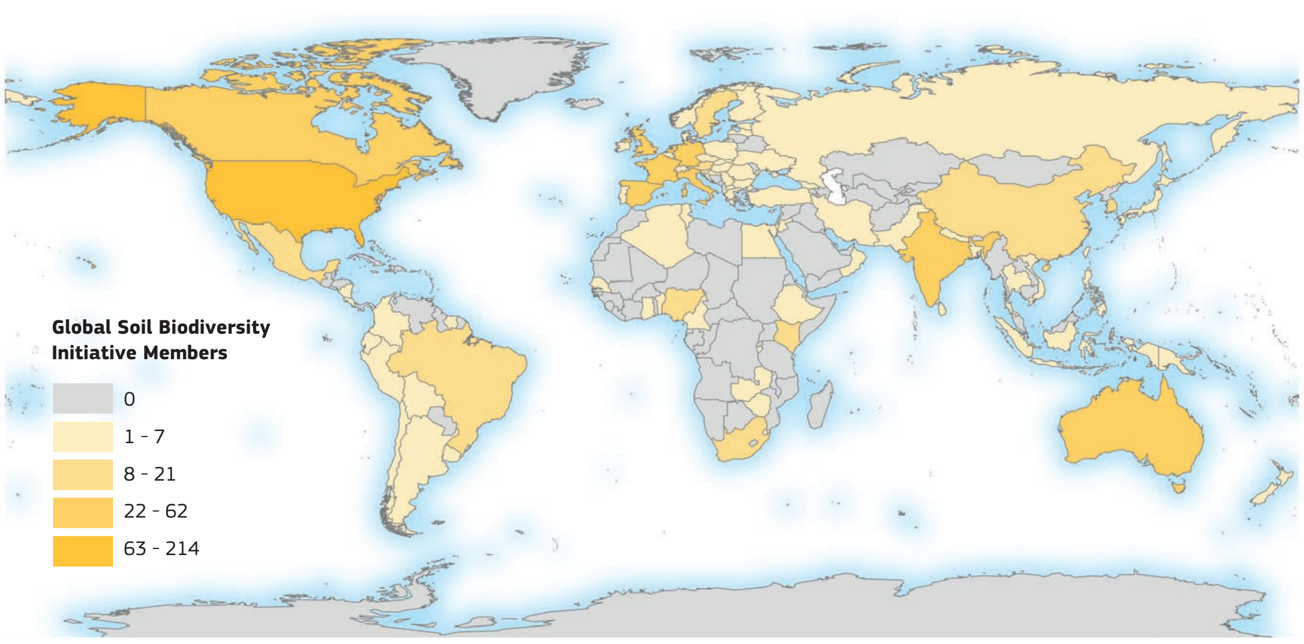
With more than 700 participants from all continents, the First Global Soil Biodiversity Conference was a great success. (TF)

Travel funds were awarded to nine early-career scientists from eight different countries, supported by the European Commission's Joint Research Centre, the International Union of Soil Sciences, Terragenome, and the United Nations Environment Programme's Global Environment Facility.

From a survey of conference delegates (264 responses):

- 54 % female, 66 % male
- 56 % early-career scientist (< 5 years post PhD)
- priorities for GSBI: global soil biodiversity assessment, platform for synthesis of soil biodiversity data, method harmonisation, a forum for developing global research networks

The 2nd Global Soil Biodiversity Conference will take place in Nanjing, China, in 2017.



Number of registered participants of the Global Soil Biodiversity Initiative (GSBI) per country as of October 2015. More than 800 people are members of the initiative. (LJ, JRC)

Global Soil Biodiversity Assessment

'When you scoop up a double handful of earth … you will find thousands of invertebrate animals, ranging in size from clearly visible to microscopic, from ants and springtails to tardigrades and rotifers. The biology of most of the species you hold is unknown…. We have little concept of how important any of them are to our existence.'

E. O. Wilson. 1987. The little things that run the world: The importance and conservation of invertebrates. Conservation Biology 1: pp. 344-346. [199]

Soil, the thin layer on the surface of the Earth, is vital for the survival of the biosphere. It is alive, with soil biodiversity providing the living basis for functioning of ecosystems. It acts as the Earth's lungs and filtering system; it is our most precious natural capital. It is of vital importance to agriculture, agroforestry, mariculture, fishing, pollution control, carbon capture and water purification, nutrient retention and cycling. In the broadest sense, soil organisms are at the core of biogeochemical cycling at both local and global scales. Our living soil is one of the keys to the maintenance of ecosystem processes and life on Earth, both on land and in the sea.

Have we made any progress in our knowledge of this diversity? Yes we have! Based on international reports, such as 'Life in the Soil – Soil Biodiversity: Its Importance to Ecosystem Processes' in 1994, the global soil biodiversity community has made enormous progress in the knowledge of taxonomy of soil biota and their role in decomposition, nutrient cycling and other ecosystem services, their intimate interactions with marine and freshwater ecosystems and their contributions to human health.

In addition to regional assessments, such as the EMEND Project in the Boreal Forest (www.emendproject.org), EcoFINDERS in Europe and BASE in Australia (see pages 158-159), the SCOPE publication 'Sustaining Biodiversity and Ecosystem Services in Soils and Sediments' and the Oxford University Press publications 'Aboveground-Belowground Linkages, Biotic Interactions, Ecosystem Processes and Global Change' and 'Soil Ecology and Ecosystem Services', have synthesised a lot of global knowledge. With the publication of the Global Soil Biodiversity Atlas, the soil biodiversity research community presents the world, from children to educators, with a portal to the wonders of life in the soil.

Yes, the global soil biodiversity community has made strides, but we recognise that a Global Soil Biodiversity Assessment is even more pressing now for the following reasons.

Why a global soil biodiversity assessment?

Since Darwin's study of earthworm activity in England, soil biodiversity and its components, their interactions with other biota and with the environment have been studied at various levels throughout the world. These data, some extensive (e.g. for Antarctica and Western Europe), some rudimentary (e.g. Southeast Asian peatlands and mangrove forests), transcend the 'black box' view of soil inhabited by an unknown and undefined set of functional groups, but these data need consolidation. Consolidation will showcase gaps in knowledge: the range of archaea, prokaryotic and eukaryotic taxa for which we lack names, classification, DNA data and trait data, the diverse linkages of soil biota to tangible functions underpinning soil-based ecosystem services, and the range in impact of climate change in different soil landscapes.

A Global Soil Biodiversity Assessment would ensure consolidation of data that are presently available on a regional or national basis, and would ensure a long-term home and available portal for this information. Most importantly though, it would highlight gaps in knowledge about soil biodiversity, and where missing data undermine the evaluation of risks and predictions of resilience that are important to society.

Soil biodiversity comprises millions of different organisms, from (**a**) ants and (**b**) mites to (**c**) myriapods and fungi. The Global Soil Biodiversity Assessment will aim at synthesising present knowledge of crucial taxonomic groups in soil, identifying how soil biodiversity and its services can be measured across the wide range of ecosystems in the world, addressing vulnerabilities of soil biota and ecosystem services and recommending future management applications based on scientific knowledge. (AM, AA, AH)

Gaps

The European Atlas of Soil Biodiversity already provided an overview of some of the information gaps in soil biodiversity both in Europe and globally [200]. These include:

- aboveground taxa in groups such as birds, butterflies and vertebrates contain detailed knowledge on the local to regional distribution of over 90 % of species, their traits and their functions, how these are changing with climate change, invasive introductions and health impacts of parasites, and the present and future threats to these taxa. These are tracked with collaborations such as eBird.org and ukbutterflies.co.uk. Such information is simply not available for any group of soil organisms, other than perhaps for earthworms in Western Europe. Other than for termites and ants, for which we know about 60 - 90 % (see page 9) of species at least to name level, knowledge about species of all other soil biota is less than 50 %, and for soil archaea, viruses, bacteria, fungi and nematodes is less than 7 %. Yet these are the taxa that support global biological and biogeochemical processes that are essential for human well-being
- data overlaying habitat type on soil type with agricultural and forestry potential is lacking, except in Western Europe and parts of North America. Nonetheless, we recognise that soils have been and are central to the development of civilisation; civilisations have risen and fallen depending on how they have nurtured or exploited their soils
- 33 % of soils are estimated to be in a state of degradation but risks to soil biodiversity locally, regionally, nationally and on an ecosystem basis are difficult to quantify. These include soil erosion risks, soil pollution risks, coastal erosion with rising sea levels, and changes in soil moisture/temperature with climate change. Presently, effective risk assessments cannot be carried out to feed into global models, such as those of the Intergovernmental Panel on Climate Change. The resilience of soil biodiversity to hazards is still unclear
- the positive and negative impacts of soil biodiversity on potential soil carbon storage are still debated

Commonalities

Knowledge on soil biodiversity and ongoing research tends to be regionally or nationally based; this is almost always because of availability of funding. Examples of research networks that provide global overviews and integration between countries are rare. The International Long Term Ecological Research (ILTER – www.ilternet.edu/research) is a good example of how to share research and data globally, with subgroups dealing with biodiversity, such as the Group of Earth Observations Biodiversity Observation Network (GEO BON – www.geobon.org). Only a few of these global research efforts consider soil biodiversity; therefore, we lack knowledge of commonalities (and differences) between the diversity in different ecosystems.

For example, temperate grasslands are the foundation of agriculture; they are where much of our food is grown. Thousands of species of microbes and invertebrates inhabit just a square metre of these temperate grassland soils, organisms whose identities and contributions to sustaining our biosphere are still largely undiscovered. Scientists know a lot about this diversity in Europe and the USA as a result of focussed research and funding in the past 25 years. For example, they can predict the impact of wildfires and overgrazing on food webs, and levels of carbon capture. However, data equivalent to those from temperate grasslands do not exist in other parts of the world or cannot be integrated. Knowledge of commonalities and differences in the components of soil biodiversity and how soil systems function globally could markedly improve predictions of soil system response to global change.

Barcoding soil life

'We have only begun to understand a small slice of the grand diversity that is life on earth and that is fast slipping through our fingers as a result of human-induced climate change, habitat destruction and exploitation.'

M. A. Goldman. 2015. Digitising the biosphere. Science 348: p. 979. [201]

International efforts to barcode life (www.barcodeoflife.org) on Earth through DNA sequencing focus to date on easily accessible aboveground biota. However, many of the antibiotics we use, types of plants that can grow, as well as decomposition, water filtration and soil development rely on soil biodiversity. We need to assess the structure and function of the global soil microbiome in a similar way as is being done in oceans with planetary scale studies on marine plankton and the Global Ocean Sampling Expedition (www.jcvi.org/cms/research/projects/gos/overview/).

A Global Soil Biodiversity Assessment would provide a focus for such an endeavour; consolidating data from GenBank, TerraGenome and again, providing a portal for soil DNA research. As the two scientists Dawn Field and Neil Davies noted 'answers to questions in the life sciences do not end with DNA – they start there'.

Conclusions

The Global Soil Biodiversity Atlas presents the first overview of soil biodiversity for both managed and natural soils on a global scale. This atlas is a remarkable international scientific effort with contributions from about 121 experts from 26 countries. The Global Soil Biodiversity Atlas was made possible through rapid advancements in scientific research on soil biodiversity that are largely due to a plethora of new technologies, including molecular tools, Internet communications, data and image sharing and storage, GPS, and perhaps most importantly, global collaborations that have developed new syntheses and understanding of the importance of soil organisms across the globe.

The designation of 2015 as the International Year of Soils 'healthy soils for a healthy life' by the United Nations emphasised soils as the foundation for all life. With unprecedented rates of global change occurring, our soils are under threat with consequences for the dynamic communities of microbes and animal species that live there. Soils, and their inhabitants, are a finite resource that must be respected and conserved. Reduction of soil biodiversity can negatively affect the quality of water, control of pests and both decomposition and nutrient cycling, with significant impacts on plant, animal and human health.

Since the establishment of the Global Soil Biodiversity Initiative (GSBI) in 2011, great progress has been made in bringing together interested parties from across the world and promoting the importance of soil biodiversity to a wider audience. The success of the First Global Soil Biodiversity Conference and the production of this atlas with the European Commission's Joint Research Centre are real examples of the power of collaboration across regions and disciplines. The Second Global Soil Biodiversity Conference will be held in Nanjing, China, in 2017, hosted by the Soil Science Society of China and the Chinese Academy of Sciences. These meetings have the potential to encourage enthusiasm about soil biodiversity research and facilitate future collaboration and research projects.

Increased education and awareness are key strategies in ensuring that soil organisms are no longer out of sight, out of mind. Through the key messages in this atlas, and efforts by the GSBI and other organisations, we aim to convince the global public of the importance of soil biodiversity to our life and economy. Because soils are under threat, we must promote interactions between scientists, policy makers and the general public in order to transfer and implement findings about the benefits of soil biodiversity and ways to restore and conserve it. Soil biodiversity is critical for soil functioning and plant production but has been largely ignored in global and regional policies that address land management, food security, climate change, loss of biodiversity and desertification.

The gaps in our knowledge of soil biodiversity in many regions around the world must be acknowledged. A global assessment is one possible method to obtain a more comprehensive understanding of the distribution of soil organisms and their functions. This information can be enhanced in the future with continued collection and synthesis of soil biodiversity data, which is urgently needed on a global scale and is required in order to develop predictive models, assess changes over time and better understand the effects of global change. Information about soil biodiversity distribution and function can be combined with other global datasets and maps, such as global carbon models, temperature and precipitation maps, desertification, land use change and climate change occurring in regions of the world.

Global Soil Biodiversity Atlas in numbers

- You are holding the 1st ever Global Soil Biodiversity Atlas (GSBA).
- The Editorial Board started working on the GSBA in 2013, and took 3 years to complete it.
- The GSBA Editorial Board consists of 27 scientists from all over the world.
- More than 100 people from 26 countries have contributed to writing the GSBA.
- There were three workshops to prepare the GSBA and thousands of e-mails sent.
- The GSBA has 8 chapters and 176 pages.
- In the GSBA you can see approximately 900 images and more than 50 maps.
- The GSBA is the 6th soil atlas of the series produced by the European Commission's Joint Research Centre.

(**a**) Chapter I of the Global Soil Biodiversity Atlas is about soil as a habitat. (**b**) Chapter II describes the wonderful diversity of soil organisms. (**c–f**) Chapter III presents the global distribution of soil biodiversity across different ecosystems. (GS/CIAT, MOL, JMA, ELE, EDU, MOK)

This atlas presents how quickly our knowledge has developed about the living organisms that help form the Earth's soils and the benefits they provide for all humans. Below we highlight some of the main findings.

Key findings

The planet's terrestrial ecosystems have a diversity of soil life, largely due to the variety of their soil habitats, which reflects the soil-forming factors of climate, parent material, topography, time and biota.

- Soil is home to thousand millions of microbes and animals that vary in shape, colour, size and function
- Scientists can now use molecular techniques to identify life (animals, fungi, protists, archaea and bacteria) in a soil sample
- Scientists are discovering new species, their distribution in soils around the world, and what they do for us
- There are many endemic species of soil microbes and animals in regions and ecosystems around the world
- Soil biodiversity is globally distributed, from pole to pole and through grasslands, forests, urban and agricultural areas
- Many types of organisms (for example, nematodes) do not follow a latitudinal gradient of greater species diversity in the tropics
- Soil properties, such as pH, largely determine soil bacterial distribution

Soil biodiversity is critical for human health: for plant growth and support, water and climate regulation, and erosion and disease control.

- Soil biodiversity consists of communities of organisms. Each soil community is unique and provides benefits for us
- Soil biodiversity is vitally important for the biogeochemical processes and ecological functioning of terrestrial ecosystems
- Soil organisms decay organic matter with relevance for soil fertility, soil structure and carbon storage
- Soil biodiversity is tightly linked to aboveground biodiversity
- Soil biodiversity provides multiple controls on above- and belowground pests and pathogens and, therefore, promotes the health of humans, plants and other animals
- Soil biodiversity enhances plant production in both managed and natural ecosystems

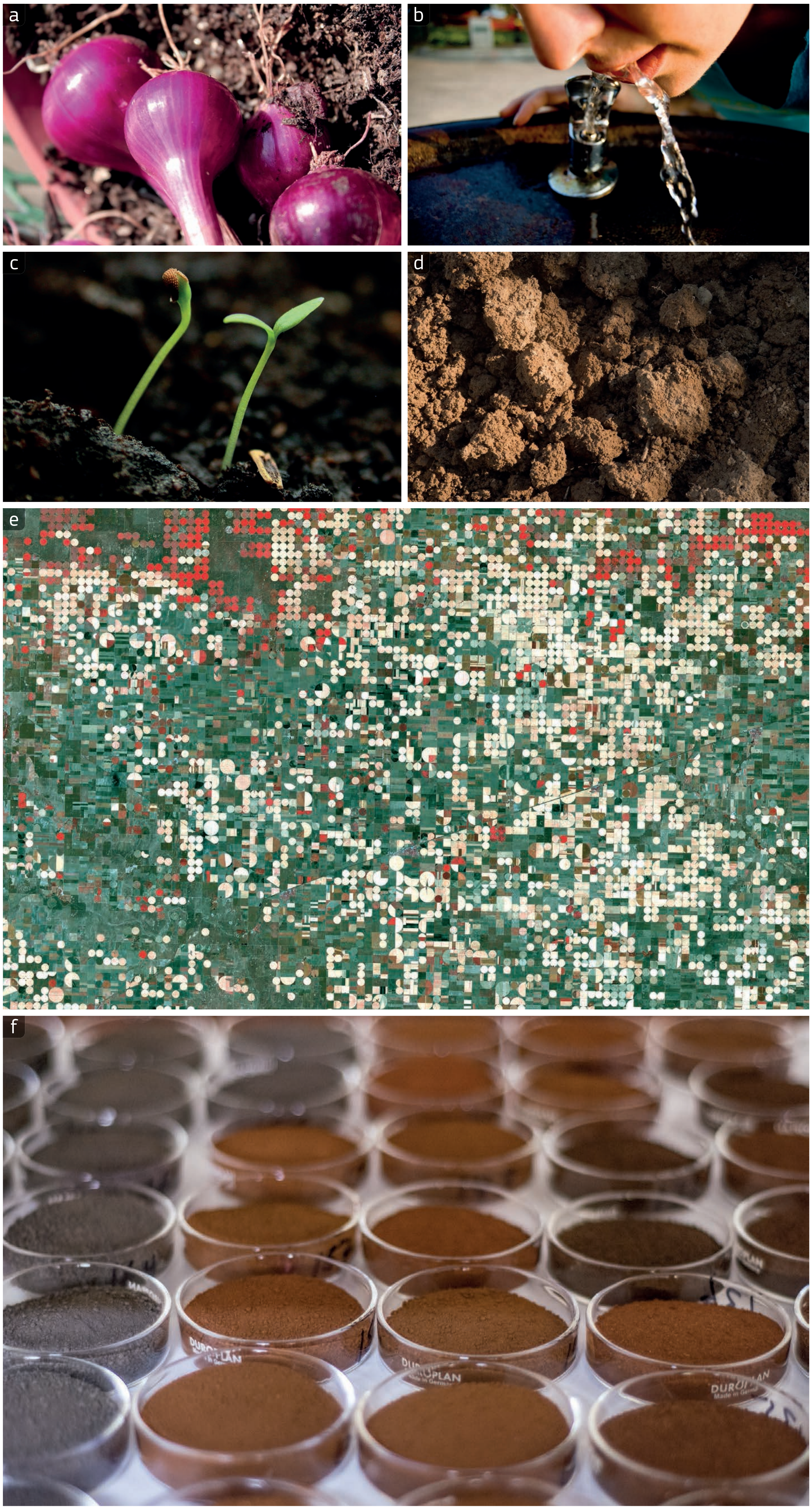
Soil biodiversity is increasingly under threat, which results in changes in the composition of soil communities and loss of species, as well as the benefits they provide to all life.

- Threats to soil biodiversity include climate change, land use change, salinisation, compaction, pollution and invasive species. These threats affect both the soil habitat and soil organisms
- Land-use change, such as intensive agriculture and sealing of fertile lands due to urbanisation, can cause declines in abundance and species diversity of many animals, including termites, earthworms, nematodes and microarthropods
- Loss of soil and its biodiversity represents a loss that is costly to nations

There is a need to celebrate these new discoveries about the life under our feet, as well as to integrate knowledge about soil biodiversity into international policies.

- The biodiversity in soils sustains the life that we see
- Reduction of soil biodiversity is a loss to society
- Measures to preserve soil biota are needed and possible
- Policies to protect and value soil biodiversity are urgently needed

Soil biodiversity is a common ground for achieving sustainability goals. Management and conservation of life in the soil is integral to governmental actions to provide healthy food, reduce greenhouse gases, lessen desertification and soil erosion, and prevent disease.



(**a–d**) Chapter IV of the Global Soil Biodiversity Atlas is about services provided by soil organisms. (**e**) Chapters V and VI describe threats to soil life and interventions to preserve it. (**f**) Chapter VII presents the importance of research and outreach in raising awareness about soil biodiversity. (HCO, DSA, BB, LCH/USDA, NASA, GS/CIAT)

ADDITIONAL INFORMATION

Glossary

This page explains some of the more technical words and phrases used in this atlas. Readers can avail themselves of additional explanations from the many comprehensive glossaries that can be found on the Internet. For example:

Technical definitions of soil terms from the Soil Science Society of America:

https://www.soils.org/publications/soils-glossary

Soil terms explained for children/general public:

http://www.soil-net.com

Texts relating to biology:

- **http://www.emc.maricopa.edu/faculty/farabee/biobk/biobookgloss.html**
- **Biology for Dummies**, Fester Kratz, R., Siegfried, D.R. John Wiley & Sons, pp. 384. ISBN: 978-0764553264

Texts relating to soil biology:

- **Earth Matters: How Soil Underlies Civilization**, 2016. Bardgett, R.D. Oxford University Press, Oxford, UK, pp. 224. ISBN: 978-0199668564
- **Soil Ecology and Ecosystem Services**, 2012. Ed. Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, T.H., Ritz, K., Six, J., Strong, D.R., van der Putten, W.H. Oxford University Press, Oxford, UK, pp. 424. ISBN: 978-0199575923

Definitions

Acid: a substance that reacts with a base, denoted by pH < 7. Substances with properties of an acid are said to be acidic

Adsorption: process by which atoms, molecules or ions are retained on the surfaces of solids through chemical or physical binding

Aerobic: living or occurring only in the presence of oxygen

Aggregate: soil particles bound together by water, organic films or biological activity. Classified by size, shape and grade (e.g. strong)

Agroecosystem: land used for crops, pasture or livestock

Algae: aquatic-based, chlorophyll-containing eukaryotic organism

Alkaline: a substance that reacts with acids, denoted by pH > 7. Also known as base

Ammonia-oxidising bacteria: group of bacteria that performs the transformation of ammonia (NH_3) into nitrite (NO_2^-)

Anaerobic: living or occurring only in the absence of oxygen

Anhydrobiotic: a type of cryptobiosis induced by a lack of water. See **cryptobiotic**

Anion: particle with a negative charge. See also **ion** and **cation**

Anthelmintic: a substance capable of eliminating parasitic worms

Anthropogenic: caused or created by humans

Arbuscular mycorrhizal fungi: fungi that form symbiotic relationships in and on the roots of host plants capable of producing tree-shaped (arbuscular) structures unique to these types of fungi

Autotroph: an organism that uses light or chemical energy to synthesise sugars and proteins from inorganic substances. Green plants are by far the most common autotrophes

Bacillus (plural **bacilli**): rod-shaped bacterium

Bacterivore: an organism that feeds on bacteria

Biochemical pathways: a series of chemical reactions occurring within a cell

Biodiversity: defined by the Convention on Biological Diversity as 'the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems'

Biofuel: fuels produced from combustible substances (e.g. plants)

Biomass: the total amount of living matter above- and belowground in an area at a given time

Biome: areas of the Earth's surface with distinct climate - flora/fauna relationships (e.g. tropical rainforest)

Biota: all of the living organisms within a given region

Bioturbation: the reworking of soils and sediments by animals or plants

Bulk density: dry mass of soil per unit volume (kg m^{-3})

Carbon: non-metallic chemical element with symbol C and atomic number 6, essential building block of all living matter. Occurs in a variety of forms (e.g. coal and diamonds). Constituent of fossil fuel and carbon dioxide

Carbon cycle: transformation of carbon dioxide into organic forms by photosynthesis, recycled through the biosphere (with partial incorporation into sediments) and ultimately returned to its original state through respiration or combustion

Carbon dioxide: naturally occurring chemical compound composed of two oxygen atoms bonded to a single carbon atom (CO_2). A gas at standard conditions. In photosynthesis, plants absorb carbon dioxide to produce carbohydrate energy. A greenhouse gas

Carbon sequestration: the fixation of atmospheric carbon dioxide in a carbon sink through biological or physical processes, for example, as organic carbon in soils

Carnivore: an organism that eats animals

Cation: particle with a positive charge. See also **ion** and **anion**

Cation exchange capacity: the ability of soil to hold nutrients used by plants, also referred to as CEC

Cephalic: directed toward or situated on, in or near the head

Chitin: a polysaccharide that is the principal component of the exoskeletons of arthropods

Chlamydospore: a thick walled asexual spore that can function as a resting spore

Chromosome: a packaged and organised structure containing most of the DNA of a living organism

Cilium (plural **cilia**): any of the short thread-like projections on the surface of a cell whose rhythmic beating causes movement of the organism or of the surrounding fluid

Clay: soil particle smaller than 0.002 mm or 2 µm

Clay minerals: clay-sized silicates (e.g. kaolinite) with an interlayer space that can hold significant amounts of water and other substances

Climate: commonly defined as the weather averaged over a long period, classically 30 years

Coccus (plural **cocci**): any bacterium that has a spherical, ovoid, or generally round shape

Commensalism: symbiotic relationship in which one species is benefited while the other remains unaffected

Comminutor: an organism that fragments the substrates on which it feeds

Confocal microscope: a light microscope with an optical system designed to obtain images of different sections of a specimen

Contaminant: an unwanted constituent in a substance that usually degrades the receiving material. Can cause damage or harm (e.g. pesticide in water) but not always (e.g. water in wine). See **pollution**

Copiotrophic: an organism that tends to be found in nutrient-rich environments

Crop: plants cultivated for food, fibre or fuel. Often grown on a large scale. Major crops include maize, wheat, rice, potatoes and cotton

Cryptobiotic: a condition in which the metabolism of an organism is reduced to an imperceptible state. Similar to an extreme form of hibernation

Cyst: a resting or dormant stage of a microorganism

Damping-off: a disease of seedlings, occurring either before or immediately after emerging from the soil, characterised by rotting of the stem at soil level and eventual collapse of the plant

Decomposer: organism that breaks down dead or decaying organisms, and in doing so, carries out the natural process of decomposition

Depauperate: lacking in numbers or variety of species

Diazotroph: a microorganism that can fix atmospheric nitrogen. See **nitrogen fixation**

Dormancy: a condition of biological rest or inactivity characterised by cessation of growth or development and the suspension of many metabolic processes

Eclosion: the emergence of an adult insect from its pupal case, or the hatching of a larva from its egg

Ecosystem: the resulting system of interactions between organisms and their environment, functioning as a unit within a given area

Ecosystem engineers: any organism that is capable of creating or modifying the local habitat

Edaphic: of, or relating to, the soil

Elutriation: a method to separate particles based on their size, shape and density

Eluviation: the movement of dissolved or suspended material within soil

Emissions: releases of substances to the environment, can be natural or man-made (e.g. the release of CO_2 during fuel combustion)

Endemic: native or limited to a certain region

Enzyme: a group of complex proteins or joined proteins produced by living cells that act as catalysts in specific biochemical reactions

Epigeous: living or occurring on or near the surface of the ground

Equatorial: located in a band around the Equator, often associated with climate that is both warm to hot and moist all year-round

Erosion: the wearing away of land or soil through one or more processes. Wind and water are the main processes affecting soil. Can be triggered by poor land management such as overgrazing or deforestation

Euedaphic: being a 'true' soil organism (i.e. particularly adapted to the soil environment)

Eukaryote: an organism, either single or multicellular, the cells of which contain a distinct membrane-bound nucleus

Eutrophication: an over-enrichment of an ecosystem by nutrients

Evapotranspiration: the transfer of moisture from the land to the atmosphere by evaporation of water and transpiration from plants

Eversible: the condition of being able to be turned inside out

Extremophile: an organism that thrives in physically or geochemically extreme conditions

Fertilisation: application of fertiliser in order to improve specific soil properties and increase soil fertility

Fertiliser: any material that is added to the soil to supply plant nutrients. Organic fertilisers are derived on the remains of plants or animal excretion (e.g. decomposed crop residues, manure) while inorganic fertilisers are either mined or chemically synthesised in laboratories

Filamentous: having the form of threads

Filopodium (plural **filopodia**): a type of pseudopodium that is extremely slender and tapers to a fine point

Flagellate: microorganism containing one or more flagella

Flagellum (plural **flagella**): a long thread-like appendage of cells or microorganisms that can be used for locomotion

Fungivore: an organism that eats fungi

Fungus (plural **fungi**): a spore-bearing, unicellular or multicellular organism lacking chlorophyll and feeding on organic matter (mushrooms are the spore-bearing fruiting body of a specific group of fungi)

Gene: a hereditary unit consisting of a sequence of DNA that determines a particular characteristic of an organism

Genotype: the genetic make-up of an organism or group of organisms

Geology: scientific field concerning the study of rocks, also used to denote solid material from which most soil is formed, characterised by the horizon symbol 'R'

Geomorphology: science of landforms

Georeference: to associate something with locations in physical space

Grazing: the regular consumption of part of one organism by another organism without killing it (e.g. cattle feeding on grasslands)

Greenhouse gas: a gas in the atmosphere that prevents heat (longwave infrared radiation) from being radiated into space. A driver of global climate change

Groundwater: water below the surface of the ground

Habitat: the native environment in which a given animal or plant naturally lives or grows

Halophile: an organism that thrives in high salt concentrations

Harvest: the process of gathering mature crops. The removal of organic matter through harvesting and subsequent transfer to market is one of the main causes of nutrient losses in soil. The harvesting of cereal crops is referred to as reaping

Hectare: metric unit of land area defined as 10 000 m^2 (i.e. 100 m by 100 m). Abbreviated to ha

Herbivore: an organism that eats plants

Hermaphrodite: an organism that contains both male and female reproductive organs

Heterotrophic: an organism that obtains carbon for growth and energy from complex organic compounds

Horizon: layer of soil or soil material approximately parallel to the surface and differing from adjacent genetically related layers in physical, chemical and biological properties or characteristics such as colour, structure, texture, pH, organic matter, etc.

Hotspot: a biogeographic region with a significant reservoir of biodiversity

Humus: organic compounds in soil, exclusive of undecayed plant and animal tissues, their partial decomposition products, and the soil biomass

Hydrogen: chemical element with symbol H and atomic number 1. A colourless, odourless, tasteless, non-toxic, highly combustible gas with the formula H_2 at standard conditions, hydrogen is the most abundant chemical substance in the Universe

Illuviation: the accumulation in one layer of soil of materials that have been leached out of another layer

Incertae sedis: a term applied to an organism or group of organisms whose relationship with others is unknown or undecided

Instar: a stage in the life of an arthropod (as an insect) between two successive moults

Interstitial: living in the spaces between soil particles

Ion: an atom which has an electric charge through having either gained or lost an electron

Land tenure: the relationship, whether legally or customarily defined, among people, as individuals or groups, with respect to land

Leaching: process by which soluble materials (including nutrients and salts) in the soil are moved deeper into the soil profile by water

Litter: fallen leaves and other decaying organic matter that make up the top layer of a soil

Maxillary: of or relating to a jaw or jawbone

Mesic: characterised by a moderate amount of moisture

Mesophile: an organism that grows best in moderate temperatures, typically between 20 and 40 °C

Metabolism: the chemical processes that occur within a living cell or organism which are necessary for life

Metagenome: the sum of genomes from all organisms within a given sample (e.g. of soil or water)

Metamorphosis: a profound change in form from one stage to the next in the life history of an organism. Also geological term for altered rocks

Methanogen: microorganism that produces methane

Micro-, meso-, macro-, megafauna: groupings of animals by size, increasing from micro-, through meso- and macro- and up to megafauna

Mineral: an inorganic component derived from rocks

Mineralisation: the process of forming a mineral by combination with another element, such as metals or oxygen

Monoculture: agricultural system that grows a single crop over a wide area, often over many years

Mycorrhiza: a symbiotic association between a fungus and plant roots

Niche: the optimal place or function of an organism within an ecosystem

Nitrate: ion with the formula NO_3^-, base of nitric acid. Combines to form highly soluble salts (e.g. sodium nitrate, $NaNO_3$). Occurs in urine and also produced by certain bacteria. Key constituent of fertilisers

Nitrification: the oxidation of ammonium compounds in dead organic material into nitrites and nitrates by nitrifying bacteria

Nitrite: ion with the formula NO_2^-, formed when nitrous acid (HNO_2) is deprotonated (i.e. removal of a proton H^+). Nitrites are used in the food preservation industry

Nitrogen: chemical element with symbol N and atomic number 7. Colourless, odourless inert gas at standard conditions. Occurs in all living organisms in amino acids

Nitrogen fixation: a process in which nitrogen (N_2) in the atmosphere is converted in the soil into ammonium (NH_4^+)

No-till: a procedure whereby a crop is planted directly into the soil without ploughing after the harvest of the previous crop

Nutrient: essential element needed by plants and animals to build biomass. Classed as macronutrients if needed in large quantities (primarily nitrogen, phosphorus, potassium, calcium, magnesium and sulphur) or micronutrients if needed in very low quantities (primarily boron, chlorine, copper, iron, manganese, molybdenum and zinc)

Nymph: the immature form of some invertebrates, particularly insects, which undergoes gradual metamorphosis

Ocellus (plural **ocelli**): a simple eye or eyespot of an invertebrate

Oligotrophic: an organism that can live in a nutrient-poor environment

Omnivore: an organism that eats both plants and animals

Organic: derived from living organisms

Organic farming: a form of agriculture in which no synthetic chemicals such as inorganic fertilisers or herbicides are used

Orogeny: process of mountain formation through the folding of the Earth's crust

Osmotrophic: that obtains nutrients by absorption, direct uptake of food compounds across membranes

Oxidation: the addition of oxygen, removal of hydrogen or the removal of electrons from an element or compound. The opposite of **reduction**

Oxide: chemical compound that contains at least one oxygen atom and one other element (e.g. NO nitrous oxide, CO_2 carbon dioxide). Most metal ore deposits are actually oxides (e.g. the iron-ore haematite, Fe_2O_3)

Palp: appendage usually found near the mouth in invertebrate organisms, the functions of which include sensation, locomotion and feeding

Parasitism: a form of interaction between two different species of organism whereby one organism, the parasite, gains a benefit at the expense of the other organism, the host

Parent material: geological or organic material from which soils are formed

Parthenogenesis: a form of reproduction in which an unfertilised egg develops into a new individual

Pathogen: any disease-producing agent, especially a bacterium or a fungus

Ped: a natural soil aggregate

Pedogenesis: process of soil formation and development

Pellicle: a thin layer supporting the cell membrane in various protists

Permafrost: ground (soil or rock and included ice and organic material) that remains at or below 0 °C for at least two consecutive years

Permeability: a measure of the ease with which fluids, gases or plant roots can travel through soil

pH: a measure of acidity, measured from 1 (acid) through 7 (neutral) to 14 (alkaline). Most soils fall in a range between pH 4 and 8

Phenotype: characteristics of an organism that are the result of the interactions of that organism's genes with environmental influences

Phoresy: association between two species in which one transports the other

Phosphorus: a highly reactive, non-metalic element with symbol P and atomic number 15. Phosphorus is never found as a free element on Earth. Essential for life as it is a component of DNA and cell membranes. Low phosphate levels limit growth in plants

Photosynthesis: process by which plant cells use the sun's energy to join carbon dioxide and water to make sugar, the food of green plants

Phylogenetics: the study of evolutionary relationships among groups of organisms

Pleomorphism: in microbiology, the ability of some unicellular organisms to alter their shape or size in response to environmental conditions

Ploughing: mechanical cultivation of soils to different depths, creating arable land

Pollution: introduction of contaminants into the natural environment that cause undesirable changes, causes stress to organic systems and can result in death of organisms depending on susceptibility or dose

Polymer: a large molecule, or macromolecule, composed of many repeated subunits

Pore: the space between soil aggregates or soil particles. Also referred to as pore space

Potassium: chemical element with symbol K and atomic number 19. Essential for life and occurs in high concentrations in plants and fruits. Intensive crop production rapidly depletes soils of potassium

Precipitation: water reaching the ground as rainfall, snow or hail

Predator: organism which hunts other organisms for food

Prey: organisms which are hunted by predators for food

Prokaryote: single-celled organism that does not contain a distinct membrane-bound nucleus

Propagule: portion of an organism that aids the dispersal of that organism and is capable of growing into a new individual

Protonymph, deutonymph and tritonymph: juvenile stages of the life cycle of mites

Pseudopodium: a temporary projection of a unicellular organism to create an appendage like protrusion for locomotion and for taking in food

Psychrotrophic: microorganism that thrives in a cold environment

Pyriscence: seed release by plants in response to fire

Reduction: the addition of hydrogen, removal of oxygen or the addition of electrons to an element or compound. The opposite of **oxidation**

Rhizosphere: zone immediately adjacent to plant roots in which levels of microorganisms can be significantly higher than that of the soil body

Rootability: the extent to which plant roots can penetrate a soil

Root exudates: carbohydrates, organic acids, vitamins and other substances released from roots

Ruderal: a plant species that is first to colonise disturbed lands

Sand: soil particles between 0.05 mm and 2 mm

Saprophagous: feeding on dead or decaying organic matter

Sclerotium (plural **sclerotia**): fungal mycelium that has hardened into a compact mass, with a store of reserve food material that in some higher fungi becomes detached and remains dormant until favourable environmental conditions for growth occur

Sediment: mineral or organic material that has been transported by wind or deposited in water (such as lakes, rivers or the sea). Basis for sedimentary rocks such as sandstone, chalk and shale

Shifting cultivation: an agricultural system in which land is cultivated temporarily, then abandoned and allowed to revert to its natural cover while the land user moves on to another location

Silt: soil particles between 0.002 mm and 0.05 mm

Sodium: chemical element with symbol Na and atomic number 11. A soft, silvery-white, highly reactive alkali metal. Sixth most abundant element in the Earth's crust and a component of numerous minerals (e.g. feldspars, rock salt). Produces highly soluble salts that are easily leached in soil

Soil compaction: a decrease in the volume of pore space between soil particles or aggregates. Severely compacted soil can become impermeable and affect plant growth

Soil depth: depth of soil body from the surface to parent material, bedrock or to the layer of obstacles to roots

Soil fertility: measure of the ability of soil to provide a sufficient amount of nutrients, water and a suitable medium for healthy plant growth

Soil function: any service, role or task that soil performs, especially sustaining biological activity (agriculture); regulating and partitioning water and solute flow; filtering, buffering, degrading and detoxifying pollutants; storing and cycling of nutrients; providing support for buildings and other structures; protecting cultural heritage

Soil organic matter (SOM): carbon-containing compounds of the soil exclusive of undecayed plant and animal residues. See **humus**

Soil productivity: the capacity of a soil to produce a certain yield of a crop under a specified farming system

Soil profile: vertical section through soil, often from surface to parent material, showing the arrangement of horizons

Soil quality: the capacity of a soil, within natural or managed ecosystem boundaries, to provide specific functions such as plant growth, maintain or enhance water quality, structural support for habitation, habitat, etc.

Soil sealing: covering or destruction of soil by urban fabric or artificial material which may be impermeable to water (e.g. asphalt or concrete)

Soil structure: aggregation of soil particles into units separated by pores

Soil texture: numerical proportion of sand, silt and clay in a soil - can be coarse (sand particles dominate), medium (silt particles dominate) or fine (clay particles dominate)

Soil/land degradation: process that leads to a deterioration of soil/land properties and functions, often caused by human activities

Sonication: disruption (as bacterial cells) by exposure to high-frequency sound waves

Species abundance: number of individuals per species in a community

Species richness: the number of species within a biological community

Spore: a small, usually single-celled asexual reproductive organism, produced by many bacteria and fungi that are capable of developing into a new individual without sexual fusion

Supercooling: the ability of organisms to lower the freezing point of liquids through the production of antifreeze molecules such as glucose and mannitol, and reducing the presence of ice-nucleating agents

Symbiosis: a close and prolonged association between organisms of two different species which may result in benefits to either or both organisms

Temperate: climatic zone that lies between the tropics and the polar regions, characterised by moderate temperatures and precipitation. Can become more extreme with distance from the ocean

Terricolous: living on or in the ground

Test: a protective shell secreted by some protists

Thermophile: an organism that thrives in warm conditions (c. 41 - 122 °C)

Topsoil: generally dark-coloured uppermost layer of soil containing decomposing organic matter, usually high in nutrients

Trophic: relating to nutrition or involving the feeding habits of different organisms within an ecosystem

Tropics: area of land around the Equator bounded by the Tropics of Cancer and Capricorn

Undulatory: moving in or resembling waves

Vacuole: a membrane-bound cavity within a cell, often containing a watery liquid or secretion

Ventral: situated on or toward the lower, abdominal plane of the body

Waterlogged soil: soil that is very wet, most pore spaces are filled with water (saturation). The opposite is an aerated soil

Weathering: the breakdown of rocks and sediments through chemical or physical (or biological) agents

Weed: vague term to define unwanted plants in human-controlled settings where they may be in competition with other plants (i.e. crops) for water and nutrients, or may interfere with harvests

Yield: the amount of a specified crop (e.g. maize and coffee beans) produced per unit area. Usually expressed in kg or tonnes per hectare

Zoospore: a type of asexual fungal spore

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If you would like to learn more about soil, we suggest investing in a general textbook. If you are interested in obtaining more information about the material presented in this atlas, the following sources are proposed. The numbers of the references listed below refer to the bracketed numbers in the text of the atlas (e.g. [6]). All urls were checked in December 2015.

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European Commission's Joint Research Centre

European
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A research-based policy support organisation

The JRC is a Directorate-General of the European Commission under the responsibility of Tibor Navracsics, European Commissioner for Education, Culture, Youth & Sport. The JRC provides scientific advice and technical know-how to support a wide range of European Union (EU) policies. More than 25 % of EU legislation has a technical or scientific basis and this trend is likely to grow as policies increasingly cut across several disciplines. The JRC, as the Commission's in-house research-based policy support centre, works to provide such support throughout the policy process, while maintaining a strong science base. Its status as a Commission service, which guarantees independence from private or national interests, is crucial for pursuing its mission.

The JRC has seven scientific institutes, located in five different sites situated in Belgium, Germany, Italy, the Netherlands and Spain, with a wide range of laboratories and unique research facilities. Through numerous collaborations, access to many facilities is granted to scientists from partner organisations. Further income is generated through the JRC's participation in Framework Progamme projects, additional work for Commission services and contract work for third parties, such as regional authorities and industry. The latest figures are available in the JRC's annual report.

https://ec.europa.eu/jrc/

JRC Activities

The JRC research programmes are decided by the Council of the European Union and funded by the EU Horizon 2020 budget. The JRC multiannual work programme, running from 2014 to 2020, focuses on clearly defined themes, reflecting a coherent approach to user needs.

JRC value statement

- 'The JRC aims to operate to the highest standards of quality, efficiency and integrity with respect to society as a whole, to its customers and to its own staff.'
- Our work ranges from detecting and measuring genetically modified organisms (GMOs) in food and feed to developing nuclear forensics technology for combating illicit trafficking of nuclear material and to using satellite technologies for monitoring land use and emergency situations such as forest fires and floods. Our activities also involve the definition of food safety standards, research into new energy technologies and evaluating policy options, for instance related to climate change.

Communicating the importance of soil and its biodiversity to children and adults during a recent Open Day at the JRC site in Ispra. (KR)

JRC mission statement

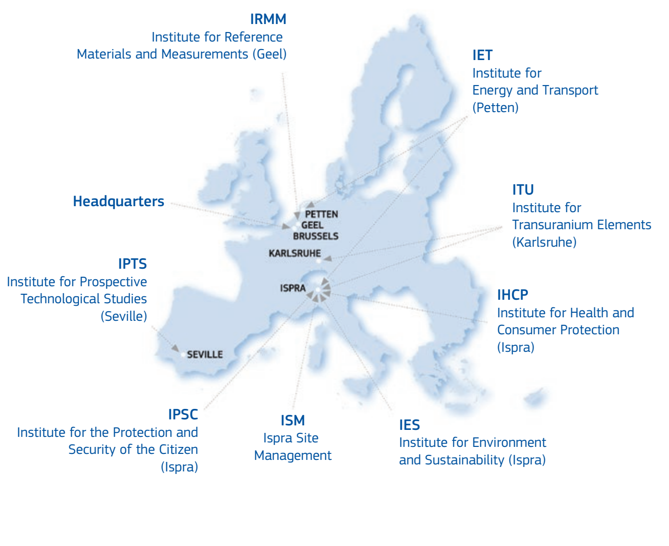
- As the Commission's science service, the Joint Research Centre's mission is to provide EU policies with independent, evidence-based scientific and technical support throughout the whole policy cycle.
- Working in close cooperation with policy Directorates-General, the JRC addresses key societal challenges while stimulating innovation through developing new methods, tools and standards, and sharing its know-how with the EU Member States, the scientific community and international partners.
- Key policy areas include: environment and climate change; energy and transport; agriculture and food security; health and consumer protection; information society and digital agenda; safety and security, including nuclear; all supported through a cross-cutting and multidisciplinary approach.

The main customers of the JRC are the policy-making Directorates General of the European Commission. Depending on the subject matter, the JRC's scientific-technical support covers the complete policy cycle or parts of it: the JRC anticipates policy needs, assesses policy options and their impacts, and monitors and contributes to the implementation of policies. It also provides operational support in certain cases, for example in anticipating environmental disasters, providing assistance to managing crises and assessing any consequential damage and their impact on human life and/or the environment. The ultimate beneficiaries of these activities are the EU Member States.

In July 2010, the JRC published its strategy for 2010-2020 with the intention to focus its efforts on seven thematic areas, which respond to major EU and global challenges and take into account the JRC's proven competencies:

- towards an open and competitive economy
- development of a low carbon society
- sustainable management of natural resources
- safety of food and consumer products
- nuclear safety and security
- security and crisis management
- reference materials and measurements

In keeping with its mission, the JRC strives to play a role as a centre of reference in its key competence areas through extensive networks with the relevant organisations in the Member States and, where appropriate, international organisations. In addition to these institutional activities, the JRC cooperates closely with external organisations. In line with a strategic approach to the JRC's role as a partner, several high-level agreements have been set up with large scientific and industrial communities on new networks and research collaboration.



The seven scientific institutes and headquarters of the JRC. (JRC)

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https://ec.europa.eu/jrc/en/institutes/ies

The Joint Research Centre. (RUG)

The Institute for Environment and Sustainability

The mission of the Institute for Environment and Sustainability is to provide scientific and technical support to the EU policies for the protection of the environment and the more efficient and sustainable management of natural resources at global and continental scales.

The Institute for Environment and Sustainability (IES) is one of the seven scientific research institutes of the European Commission's JRC.

Located in Ispra, Italy, the IES carries out research to understand the complex interactions between human activity and the physical environment, and how to manage strategic resources (water, land, forests, food, minerals, etc.) in a more sustainable manner. Together with other JRC institutes, the IES provides the scientific basis for the conception, development, implementation and evaluation of EU policies that promote the greening of Europe and the global sustainable management of natural resources. It also works in partnership with other Directorates General to support the strategic priorities of the European Commission.

The Institute brings together multidisciplinary teams who work with observations and numerical analyses, and develops the ICT infrastructures necessary to share data and models. It combines this in-house expertise with its role as a scientific catalyst in order to provide the knowledge base necessary to assess the social, environmental and economic aspects of policy options. The IES plays an active role in partnerships within the EU and global scientific communities, which are a prerequisite for finding sustainable solutions to today's global environmental challenges.

Soil at the JRC

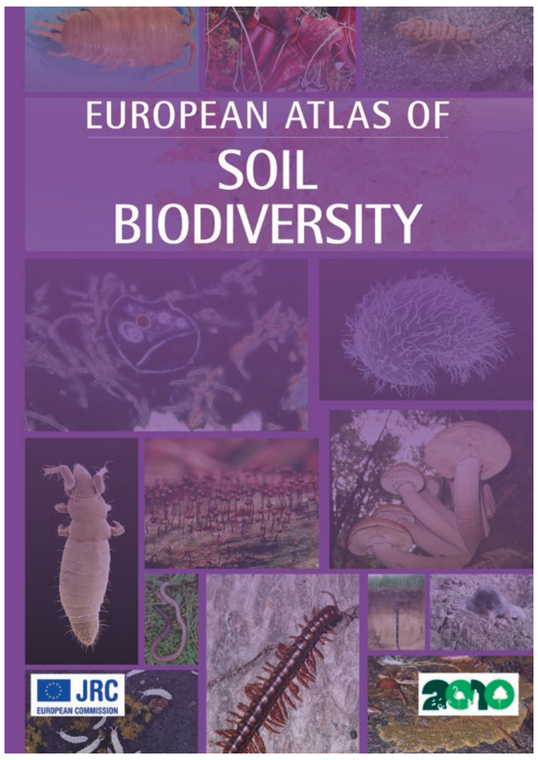
- The development of the Global Soil Biodiversity Atlas was undertaken by the Land Resource Management Unit (LRM) of the JRC's Institute for Environment and Sustainability.
- The LRM Unit investigates the balance of land-use demands and access to natural resources and maintenance of ecosystem services with a focus on understanding the components of the human environment system and trends in land condition and management, along with how these respond to changing environmental, societal and economic conditions.
- A key strength of the LRM Unit is its soil activities, which are a single focal point for soil-related data and information for European Commission services and other EU institutions. The Unit maintains the European Soil Data Centre and provides high-level analysis and assessments on the status and trends of soils in Europe and other parts of the world. The Unit is staffed by a team of soil scientists, agricultural scientists, geographers, geologists, IT specialists and modellers. There is a strong competence in soil science, spatial analysis and geostatistics.
- A key aspect of the work is collaboration with strategic partners through networking. The Soil Team of the LRM Unit supports the initiatives of the Global Soil Partnership and regional developments, the European Soil Bureau Network, EIONET-SOIL, GlobalSoilMap, the European Network for Soil Awareness, the Global Soil Biodiversity Initiative and many more.
- The Global Soil Biodiversity Atlas is a striking example of the type of high-level output generated by the JRC Soil Team. By bringing together scientists from all over the world, the atlas illustrates the benefits of international collaboration and the need for scientifically sound policies for the sustainable management of a key natural resource that is the cornerstone of food security, key environmental services, social cohesion and the economies of many countries.

Website:

http://esdac.jrc.ec.europa.eu/

JRC Soil Atlas Series

The European Commission's Joint Research Centre collaborates with soil scientists and researchers from all over the world to develop a series of soil-related atlases. To obtain a copy or for further information, please consult the Publications Office of the European Union (**http://publications.europa.eu/**) or the JRC SOIL Action's website (**http://eusoils.jrc.ec.europa.eu**).



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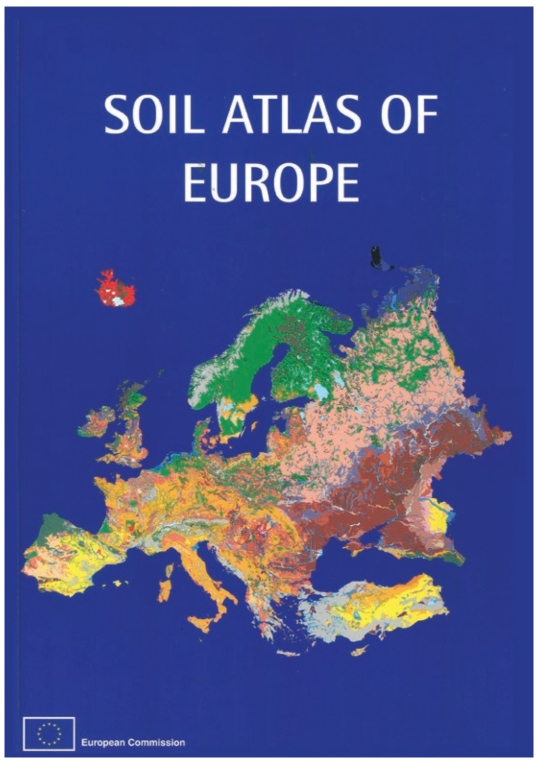

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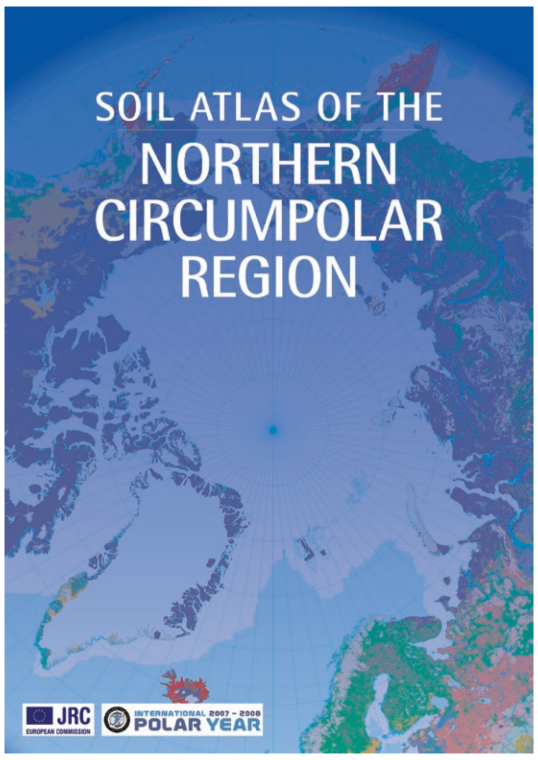

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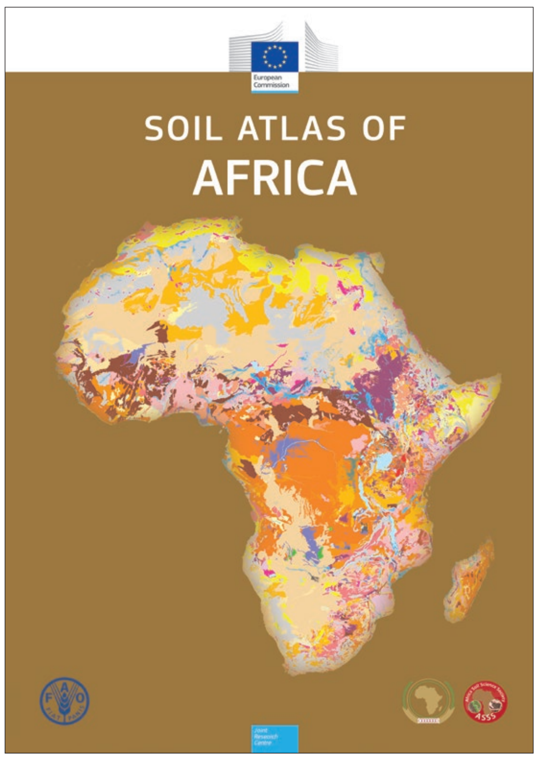

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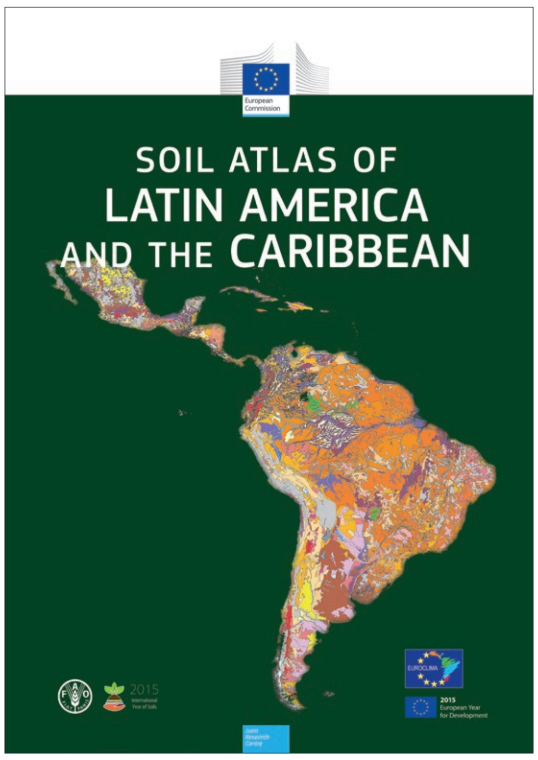

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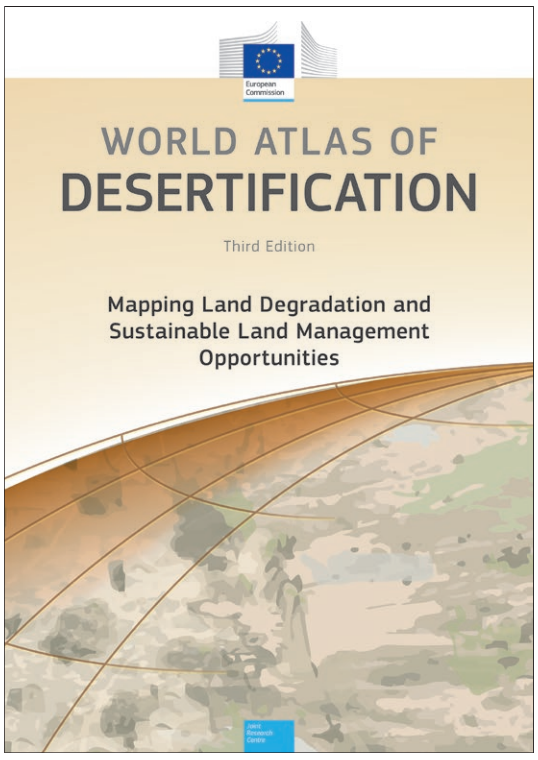

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What is soil biodiversity? How does it vary in space and time? What does it provide to society? What are the main threats to soil biodiversity? What can we do to preserve it?

The first ever Global Soil Biodiversity Atlas uses informative texts, stunning photographs and striking maps to answer and explain these and other questions.

Going through its nine chapters, every reader will learn what soils are and about the amazing creatures living in them.

You will discover the factors influencing the distribution of soil organisms, how soil biodiversity supports food production, the pressures affecting soil life and the possible interventions to preserve it.

The Global Soil Biodiversity Atlas is an essential reference to understand and appreciate the incredible world living under our feet.

Soil biodiversity is the variability among organisms living in soils.

The images above, from top left to bottom right, show representatives of the main groups of soil-dwelling organisms.
Fungi, together with bacteria and archaea, are microorganisms. (BJ)
Nematodes, together with protists, tardigrades and rotifers, are microfauna. (AM)
Collembolans, together with mites, enchytraeids, proturans, diplurans and pseudoscorpions, are mesofauna. (AM)
Earthworms, together with ants, termites, arachnids, isopods and myriapods, are macrofauna. (MK)

Soil is an extremely complex system resulting from the essential interactions between inert and living components. Soils host a myriad of soil organisms ranging in size from a few micrometres to several centimetres, from the microscopic bacteria and archaea to the "giant" earthworms and moles. All these organisms are distributed over space and time, and each ecosystem and season has its unique soil community. Soil organisms interact to provide essential ecosystem services to human beings and the environment, ranging from supporting plant growth to the regulation of climate.

Soils sustain life and are full of life. (MT)

Soils are increasingly under pressure and so are the organisms living in them. Intensive agriculture, loss of aboveground biodiversity, soil erosion and land degradation are among the most relevant threats to soil life. We can protect soil creatures by taking specific actions. No-tillage, diversification of crops, increasing reforestation and greater use of natural amendments are examples of interventions that may promote life in soils. People need to know about the fascinating world belowground and understand its value. The Global Soil Biodiversity Atlas presents the often neglected protagonists in the environment that surrounds us all.

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